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BY
A. G. TANSLEY

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WITH TEN PLATES, AND NUMEROUS FIGURES
IN THE TEXT



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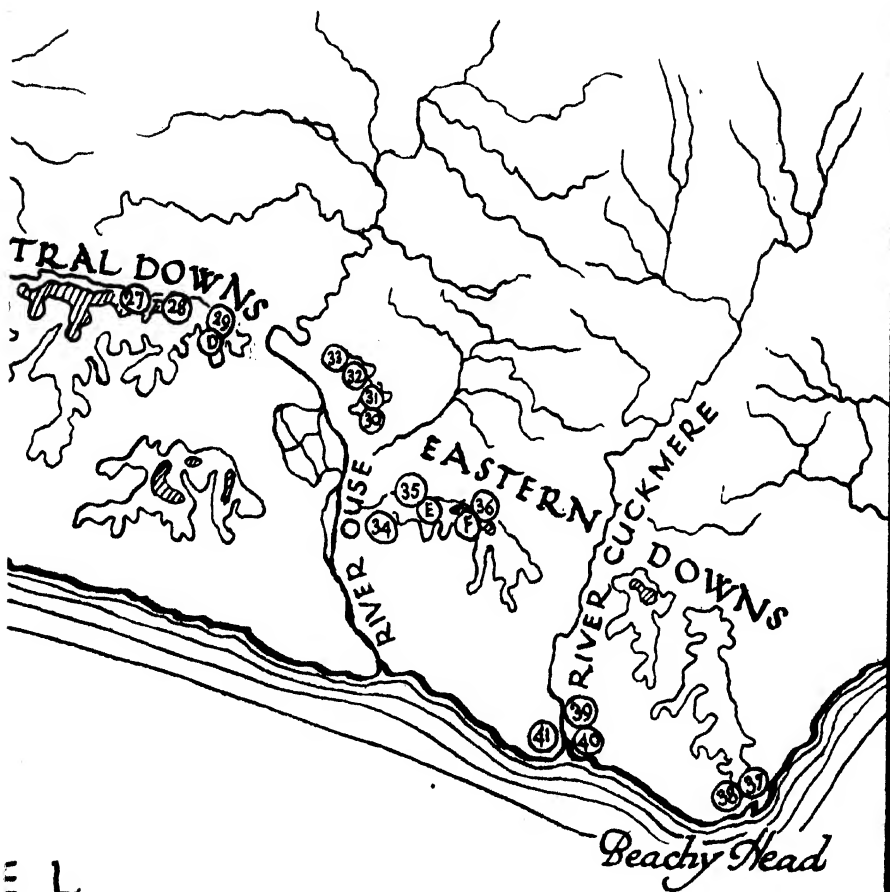
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ERRATUM

Vol. XIV, p. 165, par. 4, line 1, par. 5, line 1, and p. 166, seventh line from bottom of page.
For "phosphates" read "phosphatids."



n is that of 400 feet; 600-800 feet diagonally hatched; above 800 feet, black.
 ascribed; *a* and *b* the heaths.

ecology XIV—A. G. Tansley & R. S. Adamson "A Preliminary Survey of the Chalk Grasslands of the Sussex Downs."

STUDIES OF THE VEGETATION OF THE
ENGLISH CHALK

IV. A PRELIMINARY SURVEY OF THE CHALK
GRASSLANDS OF THE SUSSEX DOWNS

BY A. G. TANSLEY AND R. S. ADAMSON.

(With Plate I and a Sketch-map.)

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1. INTRODUCTION. DESCRIPTION OF THE REGION

The data presented in this paper were mostly collected by the authors in August, 1921, during the course of a traverse of the South Downs from War Down, just east of Butser Hill in Hampshire, to Beachy Head in Sussex, where the chalk range is cut off by the sea—a total distance, in a straight line, of 56 miles, or about 90 km. The actual course of the chalk range is somewhat longer, about 62 miles or 100 km., since it is by no means straight throughout its length. Not every mile of this distance was traversed—the most considerable gaps left being between War Down and Cocking (a distance of 10 miles), between the Devil's Dyke and Ditchling Beacon (6 miles) and between Alfriston and Beachy Head (8 miles). The line of the north escarpment of the Lower Chalk facing the Weald was mostly followed, and about 20 of the 49 areas examined were situated on the escarpment itself—the main object of the survey being to obtain data from plant communities situated on soils immediately overlying and obviously derived directly from the chalk itself over a fairly extensive stretch of country, and these are most commonly

encountered on moderate or steep slopes. A certain number of areas lying off the escarpment are, however, included in the tables, some on slopes with genuine chalk soil, others taken from "chalk heath" (6 areas) and "heath" (2 areas) developed on the chalk plateau. Data from the communities of these last two categories are given in a separate table (Table II pp. 22, 23).

The region was revisited in June, 1923, by one of the authors in company with Mr H. Gilbert-Carter, with the object of supplementing the original lists by including species not observable at the end of the severe drought of 1921. Many of the areas were re-listed and a few fresh ones listed, but little that was new was discovered, the principal species observed in 1923 and not seen in 1921 being *Senecio campestris* (*Cineraria integrifolia*), a species whose sub-aerial shoots had no doubt dried up and disappeared during the very hot summer of the earlier year. Many more records of orchids were expected in 1923, but very few were obtained.

The lists of Bryophytes are no doubt incomplete, partly owing to the season and weather of the year when they were compiled, though all the species which form important constituents of the Sussex chalk grassland are certainly included. Very little attention was given to the Bryophytes on the second series of visits. It is noteworthy that no Pteridophyte was met with on any of the 49 areas examined, with the exception of *Dryopteris filix-mas*, which had established itself along with other woodland plants on one of the heath areas (a) almost surrounded by forest. Woody plants invading the grassland have been omitted (with the exception of *Calluna*, *Erica cinerea*, *Ulex nanus* (*minor*) on the "chalk heaths" and "heaths") but have been alluded to in the short descriptions on pp. 5-14.

The approximate locations of the areas listed are shown in the Sketch-map (1-41, A-F, a, b). The sizes of the areas listed are not constant. The attempt was made to get as complete a list as possible from each place, so far as the vegetation appeared uniform and the habitat (including aspect) appeared constant. Probably the size of the area included in each list varied from about a quarter of an acre to about an acre (say an eighth to half a hectare).

The first two areas, situated in Hampshire, are selected from the lists made during the more detailed investigation by the authors of "The Chalk Grasslands of the Hampshire-Sussex border" which forms the third of these "Studies" (This JOURNAL, 13, pp. 177-223). They are as typical examples as could be chosen of the extreme western chalk grasslands of the region under consideration. These two lists are the longest of any, partly because the areas are relatively large and were visited several times in different years and at different seasons. They lie just to the west of the well-wooded western region of the Downs and are not far distant from extensive woods. Passing eastward from these there is a considerable gap in the series, extending to Cocking, but the next seven areas (3-9) are all situated on the well-wooded Western Downs, where not only much of the escarpment but great areas of

plateau, dipslope and valley side are covered with forest; and the lists show that there is no great difference between the grassland areas in this region and the two distant Hampshire ones. On the next stretch (10-18), which we have called the West-central Downs, escarpment woods are almost lacking along the western section from Amberley to the Washington gap, but are practically continuous along the eastern section, from Washington to Steyning. Here the plateau and dipslopes are almost destitute of wood but are much covered with heath and scrub, alternating with arable land. At this point too, *Bromus erectus*, very local indeed in the west, becomes locally dominant over considerable areas, and *Brachypodium pinnatum* was met with for the first time. *Filipendula hexapetala* also, so abundant on many of the Eastern Downs, had not been encountered west of this region. *Senecio campestris*, again, was not met with west of the East-central Downs, and *Phyteuma orbiculare* is much commoner in the centre and east. *Campanula glomerata*, on the other hand, was not seen east of the West-central Downs. All six of these species are characteristic of chalk grassland, so that there seems to be a real floristic transition in the region of the Central Downs, running parallel with the diminution and disappearance of chalk woodland. This does not mean, of course, that these species do not occur on the chalk of both East and West Sussex. They are all six recorded in Watson's *Topographical Botany* and *Supplement* from both, though they were not seen by us on our traverse; and the differences in their abundance and frequency on the Eastern and Western Downs must be very great.

The East-central line of Downs may be divided into three parts: a western straight portion from Beeding to the Devil's Dyke (19-26), entirely destitute of woods, a central northward curve (not examined but with a few plantations) extending to just beyond the London-Brighton road, and an eastern straight portion (27-29) from Ditchling Beacon to Mount Harry (Lewes), again with very little wood. Then we come to the isolated Mount Caburn group of Downs (30-33) just east of Lewes, and finally to the Eastern Downs beyond the Ouse valley, curving south-east and south from the Firle Beacon region to Beachy Head (34-38). The last three areas (39-41) were taken on each side of the Cuckmere valley, and, with 37 and 38, were quite close to the sea. On the escarpments of none of these Eastern Downs is there more than an occasional plantation or patch of scrub, though the plateau and dipslope are in places much covered by scrub or heath.

Apart from the wide divergence between the two ends of the South Downs in the amount of woodland they bear, there are other features of difference. The western end is at present much more generally and heavily infested with rabbits, apparently because the Western Downs are a region of great estates, largely maintained for the sporting interests of their owners, while the Central and Eastern Downs are a region of farms in which rabbits are not encouraged. This difference apparently affects the dominant grasses, *Avena pratensis* and

A. pubescens, as well as *Bromus erectus*, being much more prominent in the centre and east than in the west. *Anthoxanthum odoratum*, too, is generally a more abundant constituent of the chalk grassland east of the River Arun.

A leading physiognomic difference is the frequent occurrence in the region of the Central and Eastern Downs of tall close herbage on the steep northern slope of the main escarpment. This never exists where rabbits are abundant. It is dominated by a variety of grasses, not only the *Avenae* and *Bromus erectus*, but also locally by *Arrhenatherum elatius*, *Deschampsia caespitosa*, *Poa pratensis*, *Festuca rubra*, and in extreme cases by *Festuca elatior*, towards the damper bottom of the slope. (See areas 10, 11, 14, 19–24, 27, 28, 35, 36.) *Primula veris*, *Scabiosa succisa*, and *Rumex acetosa* are rather characteristic species of these slopes, while *Festuca ovina* and many of the small herbs of closely pastured chalk grassland are considerably diminished in abundance. The soil is generally fairly deep and often rich in humus, but it retains a distinctly high alkalinity (pH , 7.2–7.8) in the surface 2 or 3 inches. This meadow-community is distinct, as regards dominants and soil, from the well known chalk grassland dominated by *Festuca ovina*. But we see no reason to separate it from the latter at all sharply, since most of the associated list of species is the same. It is simply a result of the increase in the moist shaded conditions of the steep northern slope of the tall grasses, in the absence of continuous grazing. This leads to increased competition and a tendency to elimination of the smaller plants. The soil is characteristic (see p. 15).

Mosses are on the whole much less abundant in the grassland of the Central and Eastern than in that of the Western Downs, but some of the steep northern slopes just described carry a considerable moss flora. Nowhere, however, east of the Arun was the dominance of mosses on northern exposures of the Hampshire Downs at all paralleled, except on one northern exposure (23) of exceptionally steep slope, probably artificial and suggesting (by the presence also of *Tussilago farfara*) an early phase of development. This phenomenon is doubtless correlated with the rainfall and humidity. The Western Downs nearly to the Arun and a small area round Ditchling Beacon receive between 31 and 34 inches, while most of the Central and Eastern Downs receive between 28 and 31. The southern exposures examined are, as might be expected, notably poor in bryophytes, and some are quite destitute of them. This is specially marked in the extreme eastern region near the sea, which is also poor in flowering plants, the few submaritime species not compensating for the poor development of the general list. Areas 39, 40 and 41 are situated in a region which receives less than 25 inches of rain¹.

Besides the species mentioned on p. 3 certain others show a preponderating

¹ The rainfall data are taken from **Hall and Russell's Agriculture and Soils of Kent, Surrey, and Sussex** (1911) and represent a 10-year average. The particular 10-year period available was a dry one, and the figures are probably rather more than an inch below the averages that would result from a longer period.

distribution in east or west, according to our records. Though some of these may be devoid of distributional significance we add the more striking for what they may be worth.

Species more frequent in the east.

Anthyllis vulneraria, especially abundant around Lewes, though locally abundant here and there in the centre and west.

Arabis hirsuta, only seen in the east-centre and east.

Hippocrepis comosa, very local in the west, is met with much more frequently in the centre and east, and though always local, is quite often dominant in small areas, colouring certain downsides bright yellow in June.

Poterium sanguisorba, though one of the most constant and abundant constituents of chalk and limestone grassland in England as a whole, is not so constant in West Sussex and Hampshire as in East Sussex.

Species more frequent in the west.

Gentiana amarella on 12 (more than half) of the areas (nearly always marked as "occasional") west of the Devil's Dyke, was only seen on one area east of this point.

Helianthemum vulgare on five areas in the western, and only one in the eastern half.

Leontodon autumnalis on 11 areas in the western and only one in the eastern half.

Origanum vulgare on five in the western, one in the eastern half.

2. DESCRIPTIONS OF AREAS EXAMINED

A. WESTERN DOWNS (mostly wooded).

(London-Portsmouth Road to River Arun.)

1. *Chalton Down* (Hants). Slope 24–32° E., alt. 350 feet, side of a valley on the Upper Chalk, three miles S. of the escarpment of the Lower Chalk. Herbage 2–3 in., pastured by sheep but not too heavily. Dotted with juniper bushes, and clumps of scrub in places. Soil 4 inches to the layer of large chalk lumps and another 4 inches to fissured upper surface of chalk *in situ*.

2. *War Down* (Hants). Slope 16° E., alt. 600–700 feet. Close to escarpment of Lower Chalk. Herbage 3–4 in. pastured. A good list of mosses. Eight inches of brown to grey-brown humous loam mixed with small chalk fragments to surface of fissured chalk.

3. *Cocking*. Slope 18–20° W.N.W., alt. 500 ft., with beechwood and calcicolous coppice on one side. Herbage 1 in., rabbit eaten. *Carex flacca* leading, almost dominant, much less *Festuca ovina* than usual. *Hippocrepis comosa* locally dominant. Soil 2 in. of humous loam matted with roots: then 3 in. with chalk lumps, some 4 in. diam. Partly disintegrated chalk *in situ* at 5 in.

4. *Heyshott* (escarpment due S. of). Slope 32° N., alt. 700 ft., chalk scrub with much ash to E. and W. Herbage 2–3 in. mostly dominated by mosses,

but no great variety. Severely rabbit-eaten but somewhat protected by mosses. Frequent pure clumps of *Dicranum scoparium* 6 in. across, with leaves of *Carex flacca* (the most abundant species after the mosses) striking through; *Cirsium acaule* next in abundance. Soil 2 in. of surface, then at least 8 in. with loose chalk lumps. Seedlings of *Fraxinus*, *Cornus* and *Crataegus* nibbled over by rabbits.

5. *East Dean* (roadside, sometimes lightly pastured). Slope 10° W., alt. 400 ft. Herbage 4–8 in. (1921) 3–12 in. (1923) forming tussocks, grasses dominant. Very occasional young plants of *Corylus*. Soil a brown loam, 0–5 in. firmly held by roots, 5–10 in. with lumps of weathered chalk. Upper fissured surface of chalk *in situ* at 10 in.

6. *East Dean* (opposite 5, pastured field), slope 10–12° E., alt. 400 ft. Herbage 2–4–6 in. Turf thick. Soil a brown loam 0–5 in. held by roots as in (5), chalk *in situ* at 7 in.

7. *East Dean* (cattle-pastured grassland), slope 18° S., alt. 300 ft. Herbage 2–3 in. Mainly a chalk flora, but *Sieglingia decumbens* and *Potentilla erecta* local. Soil round roots of former gave no effervescence with dilute HCl: in other places on surface a moderate to strong effervescence.

8. *East Dean*. Enclave of grassland enclosed in North Side and Tegleaze beechwoods, alt. 500 ft. Heavily rabbit-eaten. Soil very chalky to surface. *Poterium sanguisorba* absent. Poor flora.

9. *West Burton Hill*. Slope steep to N., alt. 400 ft. Fairly typical chalk pasture with *Festuca ovina* dominant. Soil blackish brown, chalk lumps at 3 in. Chalk *in situ* at 6 in.

B. WEST-CENTRAL DOWNS. River Arun to River Adur.

10 and 11. *Amberley Mount*. West and W.N.W. exposures, alt. 400–500 feet. Thick tall grass herbage with tall inflorescences of *Avena* spp., *Arrhenatherum*, *Bromus erectus*, *Dactylis*, *Trisetum*, etc., not recently pastured. A few bushes of *Crataegus* and seedlings.

12. *Amberley Mount*. Slope 18–25° (32°) N., alt. 400–500 feet. Passing eastward to this exposure from the last the tall herbage gradually disappears as a hollow with a rabbit burrow complex is approached (untouched flowering grasses at 150 yards from this complex). Soil light brown, showing gradual transition from surface to chalk *in situ* at 12 in. Many root systems are present at this depth.

13. *Amberley Mount*, further east, slope 22–32° (34°) N., alt. 400–500 feet. Turf somewhat rabbit eaten, 2–4 in. Seedling *Quercus* and *Fraxinus*.

14. *Rackham Hill*. Slope 32–37° N., alt. 500–600 feet. Herbage 9–18 in. Tall grasses dominant, mainly *Avena pratensis*, *Dactylis glomerata* and *Agrostis alba*: inflorescences 24–30 in. Soil grey-brown with chalk lumps at 3 in. and down to 10 in. (chalk *in situ*): roots abundant to 10 in. Isolated bushes of *Juniperus*, *Crataegus*, *Fraxinus*.

15¹. *Chanctonbury* (west of). Slope 15° N., alt. 500 feet, herbage 1-3 in., moderately rabbit-eaten. Mainly a chalk flora, but *Sieglingia decumbens*, *Agrostis tenuis*, *Potentilla erecta* and *Calluna vulgaris* present. Flints and fragments of chalk at 2 in. and downward to 7 in. where chalk is *in situ*.

16¹. *Chanctonbury* (due N. of Ring). Lower part of escarpment wooded. Upper part, slope 27° N., alt. 600-700 feet. Turf about 2 in.

Poterium sanguisorba and *Carex flacca* practically co-dominant, the common mosses abundant. Seedlings of *Fraxinus*, *Corylus*, *Acer pseudoplatanus*, *Fagus*. Locally *Rubus leucostachys*. Soil looks chalky to surface, small chalk lumps in second inch. Large flat chalk blocks (probably *in situ*) with soil between from 4 to 8 inches from surface.

17¹. *Steyning Round Hill*. Slope 27° N., alt. 400-500 feet. *Bromus erectus* dominant generally, with *Brachypodium pinnatum* locally dominant. Herbage deep and thick, 9-12 in. Scattered Junipers with young *Ilex* and *Fraxinus* in their shelter: also *Viburnum lantana*, *Rosa* sp. and *Solanum dulcamara*. Soil with small chalk lumps immediately below turf, chalk *in situ* at 6 in.

18. *Steyning* (above Maudlin Farm). Slope 5° S.E., alt. 400-500 feet. Numerous mixed grasses. Scattered bushes of *Crataegus*, *Juniperus*, *Prunus spinosa*, *Rosa micrantha*, *Rubus rusticanus*. Soil very shallow, chalk showing on surface.

C. EAST-CENTRAL DOWNS. River Adur to River Ouse.

19. *Tottington Hill*. Slope 15-25° N., alt. 300-400 feet. Very good uniform grassland. Grasses decidedly dominant, *Avena pratensis* and *Bromus erectus* preponderating; then *Poterium sanguisorba*. *Primula veris* forming marked "families" and "clans." Herbage 6-8 in. Inflorescences 2-3 feet. Scattered *Crataegus* bushes. *Festuca rubra* (dominant on ant hills). Soil top 3 inches, shrinks strongly to hard black cake on drying; chalk lumps at 3 to 4 inches.

20. *Truleigh Hill*. Slope 30-32° N., alt. 600 feet. Grasses dominant. Herbage 10-12 in. Inflorescences 2 feet. Seedling *Fraxinus*.

21. *Edburton Hill*. Slope 30-35° (in steepest part) N., alt. 500-600 feet. The tall grasses (including *Poa pratensis*) and *Poterium* very abundant: *Festuca ovina*, *Bellis*, *Linum catharticum*, etc., especially in short grazed turf. Chalk lumps in soil at 4 in. Top inch of soil shrinks to blackish brown cake on drying.

22. *Perching Hill*. Slope 32-37° (in steepest part) N., alt. 400-500 feet. Slope with narrow terraces, edges occupied by tall grasses. *Festuca ovina* grazed turf between. (Cf. Cliffe Hill, Lewes, 32.) Herbage 1 (grazed) to 12 inches (tall grasses). Mosses not abundant. Soil 3 in. of surface loam with many small chalk lumps beginning 1 in. from surface. 3-7 in. disintegrated chalk. At 7 in. chalk *in situ* much fissured and broken.

23. *Between Perching and Fulking Hills*, a steep slope 37-40° (extreme 42° at steepest—perhaps cut) N., alt. 450 feet. Chalk grassland, but barely

¹ See Table I, p. 20, for rather unexpected pH values.

stable in steepest places. *Tussilago farfara* with small leaves, probably a relict of an earlier stage of succession consequent on cutting the chalk. Much moss—*Hylocomium triquetrum* and *H. splendens* locally dominant: also great quantities of *Nechera crispa* on bare patches. Over 40° the soil tends to slip and open, though mosses such as *Hypnum molluscum* and *N. crispa*, in which grow herbs and grasses, may maintain themselves on the sides of cuttings at 45° or even 50°.

24. *Fulking Hill*. Slope 22–24° N.E., alt. 400–500 feet. Herbage 4–12 in. *Avena pratensis* generally dominant, *Festuca rubra* frequent to abundant.

25. *Devil's Dyke*. Slope about 30° N.N.W., alt. 400–500 feet. Herbage 6 in. Moss layer 2 in. thick. *Achillea*, *Anthoxanthum*, *Primula veris*, *Koeleria gracilis*, *Rumex acetosa*, *Scabiosa* spp. present (absent in 26). Soil 3 in. to chalk *in situ*.

26. *Devil's Dyke*. Opposite slope, about 30° S.S.E., same altitude. Herbage 1½–4 in. Soil 2–3 in. to chalk *in situ*. Grasses only sparse, no mosses. Species mentioned under (25) absent. *Cirsium acaule*, *Hippocrepis* markedly more abundant than in (25), *Helianthemum* present. These and similar differences from (25) seem entirely a result of aspect.

27. *Escarpment due S. of Goat Farm, Westmeston* (one mile E. of Ditchling Beacon), in and above angle of V-shaped plantation. Slope 35–37° N., alt. 600–700 feet. On upper part of slope herbage 8 in., tall grasses dominant and tending to smother other plants. On lower part (between arms of V-plantation) herbage 18 in., very tall grasses overwhelmingly dominant (inflorescences 3 feet), rest of flora very poor: *Festuca elatior* generally dominant, *Arrhenatherum elatius* locally dominant: *Pimpinella saxifraga* and *Centaurea nigra* the main species maintaining themselves in the thick tall grass. This locality represents the most extreme dominance of grasses met with on a shallow chalk soil. The shelter of the plantation is evidently an additional factor. The plantation is composed of *Pinus austriaca*, *Picea excelsa*, *Quercus ilex*, *Acer pseudoplatanus*, *Fraxinus excelsior*, with *Sambucus nigra* colonising it. *Fraxinus* is the only woody plant observed to be colonising the sheltered grassland, in which *Anthriscus silvestris* occurs (rarely). Soil blackish, shrinks and hardens on drying.

28. *Escarpment N. of Plumpton Plain*. Slope 30° N., alt. 500–600 feet. Herbage 12 in. The same grasses dominant as in (27), but *Festuca elatior* not so predominant. *Crataegus* bushes scattered, with *Sambucus*. Soil very loose dark humus going down at least 8 inches, with chalk lumps almost immediately below surface.

29. *Mount Harry*. Slope 30° N., alt. 400–600 feet. (Pl. I, fig. 1.) Herbage tussocky, cattle-pastured, 6–8 in. high. Much moss. *Poterium* abundant to subdominant. Scattered *Crataegus* frequent, *Viburnum lantana* occasional, Sycamore seedlings. Soil 3 to 4 inches of dark humous loam with small chalk articles, then disintegrated chalk with soil between. Solid chalk *in situ* at 10 in.



FIG. 1. Typical pastured chalk grassland on North escarpment (Area 29, alt. 400-600 ft. with *Crataegus* shrubs and local rabbit burrows. Planted beechwood behind. Arable cultivation on Weald plain below. Mount Harry, Lewes (East-Central Downs).



FIG. 2. North escarpment of Beddingham Hill, near Lewes (Area 35), alt. 500 ft. Unpastured grassland with tall *Prunus erectus* and *Arenaria pratensis* dominant. *Pimpinella saxifraga* in flower (left foreground). Scattered bushes of *Crataegus* (Eastern Downs).



FIG. 3. Pastured chalk grassland at summit (600-700 ft.) of North escarpment, the slope of which is occupied by (probably) natural beechwood. Chantonsbury Ring (planted) in the distance (West-Central Downs).



FIG. 4. Heath on chalk plateau (Area 6, alt. 400 ft. The dark vegetation in front is *Erica cinerea*, the light strip *Brachypodium pinnatum*, the darker strip behind *Ulex nemus*. *Ilex aquifolium* on the right. South of "No Man's Land," near Steyning (West-Central Downs).

D. ISOLATED DOWNS EAST OF LEWES.

30. *Mount Caburn*. Slope 23–28° S., alt. 300–400 feet. Herbage 4 to 6 in., rather sparse. *Bromus erectus* and *Avena pratensis* dominant: these two, with *Poterium sanguisorba*, make up the great bulk of the herbage. A poor list of species and very few mosses: no bushes. Soil 2–3 inches to chalk lumps. Dries blackish, soft—many shells. Considerable carbonate and high organic content in surface layers.

31. *Mount Caburn*. Slope 23–25° N., alt. 400 feet. Herbage 8–12 in., much thicker than on (30). *Bromus erectus* dominant, with other grasses and *Poterium*. Other species more numerous and the *Hylocomia* present. One or two *Crataegus* bushes. Soil similar to (30), 2 to 3 inches to big chalk lumps.

32. *Cliffe Hill*. Slope 18° steepening to 32° downwards, S., alt. 200–400 feet. *Bromus erectus* dominant, 9 inch herbage, infl. 30 in. (very dry season of 1921 herbage 4–6 in., infl. 24 in.). On the steepest slope ridges a few inches apart, dominated by *Bromus erectus*, follow the contour lines of the hill: between these the sheep walk and browse on the turf, which shows bare chalky soil here and there. They avoid the *Bromus* on the whole (according to a shepherd they only eat the ripe seed) but here and there young *Bromus* shoots were seen eaten off. (Cf. Perching Hill, 22.) At the slope of 18° turf just continuous: large chalk lumps met with in soil at 3 inches' depth. *Crataegus* rare.

33. *Malling Hill*. Flat top, alt. 450 feet. Typical chalk flora: no alien elements. *Festuca ovina* dominant. Herbage short, pastured. Soil blackish, shrinks in drying: 4 in. to chalk, reaction neutral, high organic but low carbonate content.

E. EASTERN DOWNS (FIRLE REGION).

34. *Itford Hill*. Slope 10–15° S., alt. 200–300 feet. Herbage short, pastured. Typical chalk pasture flora. Soil 3 inches to chalk, brown, moderate organic and carbonate content, reaction distinctly alkaline.

35. *Beddingham Hill*. Slope 35° to N.E., alt. 400–500 feet. (Pl. I, fig. 2.) Herbage 12 in. Grass inflorescences 36 to 42 in. *Bromus erectus* dominant, other tall grasses and many other species associated. Mosses, mainly *Hylocomia* and *Brachythecium purum*, form a continuous stratum. Soil more than 12 inches deep. A few chalk lumps at 10–12 in. Top 4 inches with the greatest mass of roots, reaction alkaline, light grey in colour—low organic content. Seedling *Fraxinus*. Occasional plants of *Ulex europaeus*, *Rubus leucostachys*, *R. rusticanus*, *Solanum dulcamara*.

36. *Firle Beacon*. Slope 30–32° N., alt. 600–700 feet. Herbage 12 in., a mixture of tall grasses, locally eaten down by sheep. *Brachypodium pinnatum* dominant over many acres of the scarp: sometimes burned over since sheep refuse it. The *Brachypodium* shoots freely after burning, and *Pimpinella*, *Leontodon hispidus*, with *Sonchus oleraceus* and other weeds, grow between the shoots. Mosses locally abundant. Soil 3 in. of loam to disintegrated chalk.

F. EXTREME EASTERN DOWNS.

37. *Beachy Head*. Slope 20–24° to S.E. ($\frac{1}{4}$ mile from the sea), alt. 200–300 feet. Parallel ridges following the contours as in (33), turf very short between. Herbage $\frac{1}{2}$ to 6 in. Typical chalk grassland showing no maritime influence except possibly the frequency of *Daucus carota*. *Poterium sanguisorba* and *Galium verum* bulk conspicuously. Patches of scrub with *Ulex europaeus*, *Rubus rusticanus*, *Sambucus nigra*, *Prunus spinosa*, *Crataegus*, and *Rosa* spp., also *Teucrium scorodonia*, *Inula squarrosa* and *Brachypodium silvaticum*. Soil 2 inches of brown loam, grey below this. Chalk lumps at 5 inches.

38. *Beachy Head*. Flat top of cliff, alt. 500 feet. Turf very short, no tall grasses except in local shelter. Soil, locally 6 inches of brown loam with no chalk lumps: in other places chalk lumps are met with an inch or two from surface and the chalk *in situ* is at 5 in.

39. *Exceat*. Slope 5° W. on east side of Cuckmere valley one mile from the sea, alt. 50 feet. Soil alkaline, 4 inches to chalk. Poor flora, no mosses.

40. *Cliff End*. Top of cliff, alt. 200 feet, flat, some distance from edge. Herbage $\frac{1}{2}$ inch. Soil alkaline, six inches to chalk. Poor flora, no mosses.

41. *South Hill*, just west of Cuckmere Haven, alt. 150 feet. Herbage 3–4 inches, inflorescences 9–10 inches. Soil a friable loam more than 12 inches deep, moderate to strong effervescence with HCl. The top 4 inches showed the most alkaline reaction met with, pH 8.2.

Notes on the Vegetation and Flora of the Maritime Region of the Sussex Chalk.

The last five areas listed (37–41) were all fairly close to the sea (within $\frac{1}{4}$ mile except 39 which was 1 mile). The maritime influence was not, however, marked except in two negative points—the general poverty of the flora and the almost complete absence of mosses. 37, in a sheltered hollow on the east side of Beachy Head, alone had a fairly long list of species, but even here *Brachythecium purum* was the only moss seen.

The following general notes on the vegetation of this tract of country between Beachy Head and Seaford are added.

The turf on the top of the cliff edge between Beachy Head and Belle Tout (alt. 300 feet) is very short ($\frac{1}{2}$ inch), due probably in the first place to full exposure to violent winds as well as to the sun, partly perhaps to trampling. That exposure is probably the main cause is indicated by the occurrence on the sides of trenches which were dug during the war of *Teucrium scorodonia*, *Clinopodium vulgare*, etc., and the growing up of the grasses in the slightest hollow where they obtain local shelter. The general turf consists of a mixture of the commonest of the more “xerophilous” chalk grassland grasses and herbs, such as *Festuca ovina*, *Briza media*, *Cirsium acaule*, *Plantago media*, *Carex flacca*, with *Cynosurus cristatus*, *Poterium sanguisorba*, *Lotus corniculatus*, etc. There are patches of *Brachypodium pinnatum*, which suffers much, however, from exposure and trampling. The “sub-maritimes” *Erodium cicutarium* and *Plantago coronopus* were first seen here. The soil is very variable, with frequent patches of clay-with-flints passing down into soil with chalk lumps, the chalk rock lying in some cases at a considerable depth (e.g. over 6 feet).

From Belle Tout to Birling Gap and beyond to the Cuckmere valley there is a very mixed vegetation, the edaphic, biotic and local climatic conditions varying very much from place to place. There are patches of *Ulex europaeus*, the leading shrub on all this range of cliffs, often planted for cover, often burned over, and a good proportion shooting from the base of the burned

stems. *Reseda lutea* colonises the burned ground abundantly: also *R. luteola* and *Echium vulgare*. The soft young shoots of *Ulex* are much rabbit eaten. *Calluna*, *Erythraea* and *Euphrasia* are also conspicuous here. Inland the plateau is largely covered by windswept *Ulex*. *Ligustrum vulgare*, badly wind-cut, but growing vigorously, occurs, also the sub-maritime *Agropyrum pungens*.

On the top of "Seven Sisters" cliffs the intervals between the patches of *Ulex* in the hollows are filled with *Brachypodium pinnatum* which thus obtains partial shelter. In another hollow *Brachypodium* and *Bromus erectus* mixed (with some *Dactylis glomerata* and *Festuca rubra*) alternated with *Ulex*.

On the cliff in more than one place there occurred a well marked semi-open community of the following plants extending only three or four yards from the edge on four inches of soil mixed with chalk lumps under the most extreme conditions of exposure.

<i>Bromus mollis</i> forma (? nanus) dominant	
<i>Echium vulgare</i>	<i>Thymus serpyllum</i>
<i>Sedum aere</i>	<i>Plantago media</i>
<i>Hieracium pilosella</i>	<i>Anthyllis vulneraria</i>
<i>Poterium sanguisorba</i>	<i>Reseda lutea</i>
<i>Senecio campestris</i>	<i>R. luteola</i>
<i>Festuca ovina</i>	<i>Glaucium luteum</i>
<i>Cirsium arvense</i>	<i>Arenaria serpyllifolia</i>
<i>Euphorbia exigua</i>	<i>Cerastium tetrandrum</i>
<i>Bellis perennis</i>	<i>Hippocrepis comosa</i>

[The following maritime and sub-maritime plants were met with on the tops of the cliffs (100 to 200 feet) between Beachy Head and Seaford.

<i>Agropyrum pungens</i>	<i>Erodium cicutarium</i>
<i>Armeria maritima</i>	<i>Glaucium luteum</i>
<i>Carduus pycnocephalus</i>	<i>Plantago coronopus</i>

Daucus carota is locally very abundant, far more so than on any inland area examined.

On a ledge of cliff 10 feet above the beach at Cliff End (Cuckmere Haven) were *Statice limonium*, *Glyceria maritima* and *Spergularia marginata*: a little lower down *Obione portulacoides*, *Beta maritima* and *Critillum maritimum*. These formed definite local communities (Moss's "association of spray-washed rocks").]

G. "CHALK HEATHS" AND HEATHS.

The areas on which *Calluna* or *Erica cinerea* is developed (with the single exception of 15) have been excluded from Table I, and are separately listed in Table II. That no sharp line can be drawn between chalk heath and chalk grassland would be expected, and there are in fact all transitions from pure chalk grassland to typical "chalk heath" (perhaps also from this to true heath, though this point has not been studied). While such plants as *Sieglingia decumbens*, *Agrostis tenuis* and *Potentilla erecta* may occasionally be found in good chalk grassland such as is developed on fairly steep slopes or on narrow ridges, it is apparently the rule that on very gentle slopes and flat surfaces, *Calluna* eventually appears and the other species mentioned increase in abundance, though most of the chalk grassland plants normally remain, as is shown clearly enough by the fact that the general list of species in Table II differs very little from that in Table I. This gives the mixed community which has been called a "chalk heath." Whether it would normally develop into a true heath with elimination of the characteristic chalk grassland plants is a question that has not been investigated. The pH determinations made on the soil samples collected are below pH 7 in the top layer of soil of the four "chalk

heaths" given in Table II whose soils were tested. In another instance, however (Buddington Farm—see below), the pH of the top inch was 7.0.

Chalk heath areas examined (*A, B* in well-wooded, *C, D* in slightly-wooded, *E, F* in non-wooded region).

A. Heyshott Down. Summit, flat, 700 feet. At the highest level of the summit there was a vegetation of *Calluna* (v.a. to d.) with *Dicranum scoparium* and *Agrostis tenuis* on 4 inches of loam with a pH value of 6.9. Below this were flints and then (5–9 in.) flints mixed with disintegrated chalk lumps to chalk *in situ* at 9 inches. Isolated bushes of *Crataegus*, *Rubus idaeus* and *Rubus* sp.

At a slightly lower level but still on the flat summit of the Down was a vegetation composed mainly of the common chalk grassland plants, but with *Potentilla erecta*, *Luzula campestris*, *Dicranum* and *Cladonia* conspicuous. The turf was half an inch deep with two inches of soil, then three inches with numerous small chalk lumps, and chalk *in situ* at five inches.

B. Burton Down. Summit, flat to 10° S., close to woodland, alt. 700 feet. Turf very badly rabbit eaten, $\frac{1}{4}$ inch, of *Festuca ovina*-*Agrostis tenuis*; only where mosses (*Hylocomia*, *Dicranum*, etc.) occurred was there a herbage depth of two inches. The clumps of *Calluna* were severely eaten back. A little distance away *Calluna* was less eaten 12–18 in. high, flowering. Scattered *Ulex europaeus*, *Crataegus*, *Rosa lulitiana*, *Rosa* sp. and *Fraxinus*. Soil 4 in. of brown loam, then 6 inches with flints and 2 inches with chalk lumps. Chalk *in situ* at 12 inches. (On east slope stiff yellow clay with flints to at least two feet.)

C. Plateau between Steyning Round Hill and No Man's Land. Alt. 500 feet. Light brown very friable dry loam mixed with flints and a few very small chalk fragments. Practically uniform to 16 inches (chalk *in situ*). Roots abundant to 4 inches, still frequent at 12 inches, some penetrating to chalk. Bushes of *Crataegus*, *Juniperus*, *Rubus leucostachys*, *Prunus spinosa*. Mosses generally absent (*Brachythecium rutabulum* local).

This is not a chalk heath; on the contrary it has a pH value of 7.4, and none of the chalk heath plants except *Agrostis tenuis*, but is included as a flat plateau area for comparison with the others. Possibly it has been ploughed at no distant date.

[On the Chanctonbury plateau, east of Buddington Farm at an altitude of 600 feet there is good chalk heath with the following species on the comparatively shallow soil (7 inches) overlying the chalk:

<i>Calluna vulgaris</i>	co-d.	<i>Hieracium pilosella</i>	f.
<i>Festuca ovina</i>	co-d.	<i>Lotus corniculatus</i>	o.
<i>Poterium sanguisorba</i>	a.	<i>Taraxacum erythrospermum</i>	o.
<i>Ranunculus bulbosus</i>	a.	<i>Carex flacca</i>	o.
<i>Cirsium acaule</i>	a.	<i>Potentilla erecta</i>	o.
<i>Plantago lanceolata</i>	f.—a.	<i>Agrostis tenuis</i>	o.
<i>Filipendula hexapetala</i>	f.	<i>Avena pratensis</i>	o.
<i>Thymus serpyllum</i>	f.	<i>Luzula campestris</i>	o.
<i>Veronica officinalis</i>	f.	<i>Achillea millefolium</i>	o.
<i>Leontodon hispidus</i>	f.	<i>Trifolium repens</i>	o.
<i>Polygala vulgaris</i>	f.	<i>Linum catharticum</i>	o.

The following are the results of analysis of the 7 inches of soil overlying the chalk:

Depth of sample	pH value	Water loss of air dry soil at 100° C.	Loss on ignition	CaO	MgO	K ₂ O
0"-1"	7.0	7.5	22.8	1.12	.52	.32
0"-3"	7.2	6.7	18.9	.74	.53	.31
3"-7"	7.5	6.3	16.0	.78	.58	.28

On the adjoining plateau *Calluna* and *Helianthemum* together occupied many mole heaps.]

D. Mount Harry. Flat top, alt. 600 feet. Variable short turf ($\frac{1}{2}$ -4 in.) cattle pastured and some rabbits, with *Calluna*, *Agrostis tenuis*, *Sieglingia decumbens* and *Potentilla erecta*, and also a number of ordinary chalk grassland plants: occasional bushes of *Ulex europaeus* and *Crataegus*, *Fraginus* seedling. Soil 4 inches of dark humous loam with a few flints, shrinking to a cake on air drying, overlying chalk at 4 inches. Surface 2 inches markedly acid (pH 6.0 to 6.5), rich in organic matter and poor in carbonates.

E. Beddingham Hill plateau. Alt. 600 feet. Grasses and clovers conspicuous, the Avenae and *Bromus erectus* absent. *Calluna* (and elsewhere *Erica cinerea*) abundant locally. *Ulex europaeus* and *Rubus* spp., *Mespilus germanica* in scrub. Soil 3 inches of loam, then flints to over 8 inches from surface.

F. Firle Beacon plateau, close to edge of escarpment. Alt. 700 feet. Good chalk heath. Soil 6 inches of sandy loam, pH 6.9.

The plateau and dipslope ridges running south from the Firle Beacon massif are largely covered with loam and flints and bear rough scrub in which *Rubus* spp. and *Ulex europaeus* are prominent, with *Calluna* and *Erica cinerea* alternating. *Ulex nanus* (*minor*) occurs among the *Calluna*. There is also a great deal of *Brachypodium pinnatum* in patches. Arable land alternates with the waste, and from this *Cirsium arvense* often invades. The whole region is very similar to the Chanctonbury-Cissbury region 22 miles to the west.

Three-quarters of a mile to the south-east of area F *Calluna* (in isolated tufts, eaten back) gets 40 yards down over the edge of the plateau in the closely eaten turf of the escarpment slope at an angle of 20°. This is the maximum angle of chalk slope on which *Calluna* has been found.

Heaths. Two areas which may fairly be called "heaths" without the prefix "chalk" were listed—the summit of Graffham Down in the well-wooded western area, and an area south of "No Man's Land" on the Chanctonbury-Cissbury plateau. Both of these show relatively high acidities, values below pH 6, and an absence of many of the chalk grassland plants.

a. Graffham Down. Flat, on the plateau close to the top of the escarpment, alt. 700 feet, in an angle of forest. Here *Erica cinerea* is abundant to dominant and *Calluna vulgaris* locally abundant. But between these dwarf shrubs there are patches of rabbit-eaten turf. There is an abundance of scattered

bushes and young trees, the area clearly being on the way to develop forest. The following woody plants occurred:

<i>Cornus sanguinea</i>	<i>Lonicera periclymenum</i>	<i>Salix cinerea</i>
<i>Crataegus monogyna</i>	<i>Prunus spinosa</i>	<i>Sorbus aria</i>
<i>Fagus sylvatica</i>	<i>Rosa micrantha</i>	<i>Ulex europaeus</i>
<i>Fraxinus excelsior</i>	<i>Rubus leucostachys</i>	<i>Viburnum lantana</i>
<i>Ligustrum vulgare</i>		

There is a long list of herbaceous plants—a mixture of chalk grassland and heath species, with a few woodland forms: namely, *Digitalis purpurea*, *Dryopteris filix-mas*, *Epilobium angustifolium*, *Potentilla sterilis*. The last named are omitted from the list in Table II.

Though Graffham Down summit is on the whole a heath, it contains a certain admixture of chalk grassland elements. The soil is a dry light loam mixed with flints. The top 4 inches are very poor in carbonates and the pH value obtained was 5.8. There is no visible sign of chalk to a depth of one foot, but at this level chalk lumps occur.

b. Heath south of "No Man's Land" (Chanctonbury). Alt. 400 feet, slope 5° to S.E. (Pl. I, fig. 4.) This area was dominated by alternating patches of *Erica cinerea* with *Ulex nanus* and patches of *Brachypodium pinnatum*: scattered bushes of *Crataegus*, *Sambucus nigra*, *Ulex europaeus*, *Rubus caesius*, *R. leucostachys*, *R. rusticanus*, *Rosa canina*, *Ilex* and *Fraxinus*, with *Clematis vitalba*. Soil a light-brown dry friable loam inclined to be clayey at 6 in.: at 8 inches a few flint fragments. The pH value of the top 8 inches was 4.6.

In comparing the lists from these chalk-heath and heath areas with those from the chalk grasslands we see that the occurrences and abundance of such characteristic chalk grassland species as the *Avenae*, *Bromus erectus*, *Koeleria gracilis*, *Scabiosa columbaria*, *Pimpinella saxifraga*, *Phyteuma orbiculare*, are more or less diminished on the chalk heaths, while all these except *Pimpinella* are quite absent from the heaths, as well as *Linum catharticum* and *Bellis perennis*. On the other hand, in addition to the appearance of *Calluna*, there are increased occurrences and abundance on the chalk heaths of *Agrostis tenuis*, *Carex caryophylllea*, *Holcus lanatus* (to some extent) and *Sieglingia decumbens*.

On the heaths appear, besides *Calluna* and *Erica*, *Carex pilulifera*, *Hypericum pulchrum*, *Hypochaeris radicata* (found in only one of the 41 grassland areas), *Stachys betonica*, *Galium saxatile*, *Ceratodon purpureus*. *Polytrichum juniperinum* and *Hypnum cupressiforme* var. *ericetorum*, too, appear on the heaths and on one of the chalk heaths.

But the great majority of all the species are common to the three communities. It is clear that the chalk heath cannot be regarded as more than a modification of chalk grassland in the direction of heath, while the two genuine heaths on the chalk plateau have a poor list of heath species. They may be regarded as "association-fragments" in the sense of the Upsala and new Zürich schools, strongly influenced by the flora of the surrounding chalk grassland. It is only locally that the "leaching" plateau succession has developed heath.

3. FLORA AND SOILS OF THE AREAS

The two following tables (pp. 16-23) record the data collected.

4. SOILS OF CHALK GRASSLAND

The areas of chalk grassland from which the data presented in this paper are taken were all situated, as already mentioned, on comparatively shallow soils overlying and obviously directly derived from the chalk itself. Small single samples of the soil were taken from a majority of these areas (in three cases two samples from each) and the results of the partial analyses of these are given in Table I. Nearly all the samples were taken from the layer of maximum root development: the actual depths are given in the table. Such data are of course quite inadequate as the basis of a general account of the chalk grassland soils as such, but some comparative remarks may suitably be made here.

Broadly speaking three types of soil were met with: (1) a *grey powdery soil* with a very high calcium content, and varying in tint according to the humus content, which was often high, (2) a *brown loam*, also with a high average humus content, and (3) a *dark coloured sometimes black soil*, very rich in humus and shrinking to a tough compact cake on drying. Of these (2) is the commonest and (1) the rarest, (3) occurring exclusively, in our experience, on steep northern escarpment slopes bearing tall herbage. In one or two cases a grey soil occurred under tall herbage. This may very well be due to intermittent heavy grazing checking the accumulation of humus, but the point could not be determined without far more field study than we could give.

		CaO		Loss on ignition		pH	
		Average	Range	Average	Range	Average	Range
(1)	6 grey soils	29.1	21.7-37.9	24.6	11.6-31.6	7.4	6.5-7.9
(2)	6 brown soils	18.1	9.3-27.4	25.9	20.5-32.7	7.4	6.9-7.6
(3)	7 dark soils	15.0	2.4-25.8	31.3	23.5-42.6	7.5	7.2-7.8

It is clear that the grey soil is the most primitive, though the areas examined, all of which bore pretty fully developed chalk pasture, are none of them so primitive as the Buriton Limeworks (*a*) soil (see No. III of these "Studies," This JOURNAL, 13, p. 184), which contained far more calcium and far less humus than any of those considered in the present paper. Transitional soils between (1) and (2), grey-brown in colour, were met with, and also between (1) and (3), blackish-grey. These last dried black, or nearly black, but soft and powdery, while the typical dark humous soils (3) dried into a tough black or dark brown cake with considerable shrinkage.

It seems, therefore, that while the dark humous soils (3) are derived from (1) under conditions of moisture and rank growth of herbage, the brown soils (2) are formed from (1) under conditions of pasturage, and greater dryness. These brown soils are the most widespread and occur on medium and also

Table I.

Aspect Slope	Life- form	Western Downs (mainly wooded) (Cocking gap to River Arun)									West-central Downs (River Arun to River A.								
		Extreme W.																	
		E.	E.	N.N.W.	N.	W.	E.	S.	N.		W.	W.N.W.	N.	N.	N.W.	N.	N.	N.	N.
		24- 35°	16°	18- 20°	32°	10°	10- 12°	22°					18- 32°	22- 32°	32- 37°	15°	27°	27°	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
<i>Aceras anthropophora</i>	G	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Achillea millefolium</i>	H	f.	o.	—	o.-f.	f.-a.	—	o.	o.	—	o.	—	o.	f.	f.	o.-f.	f.	f.	
<i>Agrimonia eupatorium</i>	H	r.	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Agrostis alba</i>	H	—	o.	o.	f.-a.	o.-f.	f.	—	—	—	a.	f.	o.	—	a.	o.	—	l.a.	
<i>A. tenuis (vulgaris)</i>	H	l.a.	a.	—	—	o.	—	—	o.-f.	—	—	—	—	—	—	a.	—	—	
<i>Anthoxanthum odoratum</i>	H	f.	o.	—	—	f.	f.	—	—	f.	a.	f.	f.	o.	o.	a.	f.	—	
<i>Anthriscus silvestris</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Anthyllis vulneraria</i>	H	l.a.	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—	—	
<i>Arabis hirsuta</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Arenaria serpyllifolia</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Arrhenatherum elatius</i>	H	—	—	—	—	—	—	—	—	—	l.	l.	—	—	l.	—	—	l.a.	
<i>Asperula cynanchica</i>	Ch	f.	f.-a.	f.	f.	f.	f.	o.-f.	o.	f.	f.	f.	o.	o.	o.	o.	o.-f.	o.	
<i>Avena pratensis</i>	H	l.a.	l.	o.	—	f.-a.	f.	f.-a.	o.	o.	a.	l.a.	l.	l.a.	v.a.	o.	o.-f.	a.	
<i>A. pubescens</i>	H	l.a.	—	l.	l.	f.-a.	f.	—	—	f.-a.	f.	f.	o.	—	—	o.	o.-f.	l.a.	
<i>Blackstonia perfoliata</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Bartsia odontites</i>	Th	—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Bellis perennis</i>	H	o.	o.	o.	o.	o.	o.-f.	—	o.	o.	o.	o.	o.	o.	—	o.	o.-f.	—	
<i>Brachypodium pinnatum</i>	H or Ch ¹	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.d.	
<i>B. silvaticum</i>	H	—	—	l.	—	—	—	l.	—	—	—	—	—	—	—	—	l.	—	
<i>Briza media</i>	H	f.	o.	o.-f.	f.	f.	a.	f.	f.	o.	f.-a.	f.	f.	o.-f.	f.	o.	f.	f.	
<i>Bromus erectus</i>	H	l.	—	—	—	l.	o.	—	—	—	l.	l.	—	—	l.	—	—	d.	
<i>B. mollis</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Calluna vulgaris</i>	Ch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	
<i>Campanula glomerata</i>	H	o.	—	o.	—	o.	f.	—	—	—	—	—	r.	—	—	—	—	—	
<i>C. rotundifolia</i>	H	f.-a.	o.-f.	f.	f.	f.	f.	l.a.	o.	—	f.	f.	o.	f.	o.	f.	f.	f.	
<i>Carex caryophyllaea</i>	G	o.	o.	f.	o.-f.	—	o.-f.	—	f.	—	o.	f.	o.	o.	—	o.	f.	—	
<i>Carex flacca (glauca)</i>	G	a.	v.a.	v.a.	a.	f.	f.-a.	v.a.	v.a.	a.	o.-f.	f.-a.	a.	a.	f.	f.	v.a.- c.d.	a.	
<i>Carlina vulgaris</i>	H	o.	o.	o.	—	o.	o.	—	r.	—	—	—	—	o.	—	o.	o.	—	
<i>Caucalis anthriscus</i>	H	—	—	—	—	—	—	—	—	—	o.	o.	—	—	—	—	—	—	
<i>Centaurea nigra</i>	H	l.	—	o.-f.	—	a.	—	—	—	—	o.	o.	f.	o.	o.	—	—	o.	
<i>C. scabiosa</i>	H	—	—	—	—	o.	—	—	—	—	—	—	f.	o.	o.	—	—	—	
<i>Corastium vulgatum</i>	Ch	l.	o.	—	—	l.	—	—	—	—	—	—	—	—	r.	—	f.	—	
<i>Cirsium acaule</i>	H	f.-a.	f.- v.a.	a.	a.	f.-a.	a.- v.a.	v.a.	v.a.	a.	f.	a.	a.	a.	a.	f.	f.- l.a.	o.-f.	
<i>C. arvense</i>	G	—	—	—	—	—	—	r.	a.	—	—	—	—	l.	—	—	—	—	
<i>C. lanceolatum</i>	H	r.	r.	—	—	r.	—	—	—	—	—	—	—	l.	—	—	—	—	
<i>C. palustre</i>	H	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	
<i>Clinopodium vulgare</i>	H	l.	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Crepis virens</i>	Th	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Cynoglossum officinale</i>	H	l.	—	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	
<i>Cynosurus cristatus</i>	H	a.	—	—	—	o.-f.	o.-f.	l.	—	—	f.	—	—	—	l.	—	o.	—	
<i>Dactylis glomerata</i>	H or Ch ¹	l.	l.	—	—	o.-f.	o.	—	—	—	l.a.	l.	l.	l.a.	a.	—	l.a.	a.	
<i>Daucus carota</i>	H	o.	—	o.	—	r.	—	o.	—	—	l.	—	—	—	—	—	—	—	
<i>Deschampsia caespitosa</i>	H or Ch ¹	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	—	—	l.	
<i>Echium vulgare</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Erythraea centaureium</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Euphrasia nemorosa</i>	Th	o.	o.-f.	f.	f.	o.	r.-o.	f.-a.	o.-f.	—	—	o.	f.	—	—	f.	o.	o.	
<i>Festuca elatior</i>	H or Ch ¹	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>F. ovina</i>	H	v.a.	v.a.- d.	f.-a.	a.	a.	f.	v.a.	v.a.- d.	d.	v.a.	a.	v.a.	v.a.	a.	v.a.	v.a.	a.- s.d.	
<i>F. rubra</i>	H	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Filipendula hexapetala</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	l.	—	
<i>Fragaria vesca</i>	H	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	
<i>Galium erectum</i>	H	l.	l.	—	o.	—	—	—	—	—	—	—	l.	l.	o.	—	o.	—	
<i>G. mollugo</i>	H	r.	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	
<i>G. verum</i>	H	a.	o.	—	—	f.	f.	—	—	f.	o.	o.	o.-f.	—	l.	f.	o.	f.	
<i>Gymnadenia conopsea</i>	G	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	

¹ These tufted grasses, though classed by Raunkiaer as hemicryptophytes, may, in our climate, have perennating b above the soil surface.

Table I.

East-central Downs (River Adur to River Ouse)														Mount Caburn group east of Lewes				Eastern Downs										Occurrence	
N. 15- 25°	N. 30- 32°	N. 30- 35°	N. 32- 37°	N. 37- 40°	N. 22- 24°	N.N.W. 30°	S.S.E. 30°	N. 35- 37°	N. 30°	N. 30°	S. 23- 28°	N. 23°	S. 18- 32°	Flat	S. 10- 15°	N. 30°	N. 30- 32°	S.E. 20- 24°	Flat	W. 5°	Flat	S.	No. of areas	%					
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	31	2					
a.-	f.	f.	f.	—	f.-a.	o.-f.	—	f.	a.	o.	—	f.	o.	o.	o.	f.	f.	f.	f.	—	—	l.a.	31	76					
l.v.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	4	10					
f.	o.	—	l.a.	—	a.	—	—	f.	a.	l.a.	—	—	—	—	—	f.	l.a.	f.	—	—	—	—	22	54					
v.a.	a.	f.	f.	a.	l.v.a.	f.	—	a.-l.d.	l.a.	f.	—	l.	f.	o.	—	f.	—	f.	o.	—	—	—	28	70					
l.a.	—	—	—	—	—	—	—	r., l.	—	—	l.a.	o.	o.	o.-f.	f.	—	r., l.	l.f.	—	—	o.	o.	2	5					
—	—	—	—	—	o.	r.	—	o.	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	12	30					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10					
l.	o.	—	o.	f.	f.	—	—	l.v.a.	—	—	—	l.	—	—	—	l.	—	a.	a.	—	—	—	9	22					
o.-	f.	—	—	—	—	—	—	—	a.	f.	a.	a.	a.	—	—	a.	l.a.	a.	a.	—	—	—	31	76					
v.a.-	v.a.	o.	v.a.	v.a.	—	a.	a.	v.a., l.d.	l.v.a.	v.a.	a.	a.	a.	o.	o.	a.	l.a.	l.a.	a.	f.	—	v.a.-	39	95					
d.	—	—	—	—	—	—	—	l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—	c.d.	—	—					
a.	a.	v.a.	—	f.	v.a.-	a.	—	a.	d.	o.	a.	a.	a.	r.-o.	l.f.	f.	o.	—	—	—	—	—	28	70					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	1	2					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	65					
o., l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	20					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12					
a.	a.	o.	f.	r.	f.	f.-a.	f.	f.	l.	a.	—	o.-f.	f.	o.-f.	f.	f.	f.	f.	f.	f.	a.	a.	39	95					
l.a.	l.a.	—	—	—	—	—	—	l.a.	l.v.a.	l.	d.	d.	d.	f.	l.	d.	l.	—	r.	d.	f.	—	25	62					
l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12					
f.	a.	—	o.	o.	o.	—	—	f.	f.	o.	—	—	f.	—	—	o.	—	—	—	—	—	—	27	67					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	52					
o.	a.	o., l.	v.a.	a.	f.	f.	—	r.-o.	l.a.	o.	a.	r.-o.	f.	a.	a.	v.a.	a.	f.	a.	a.	o.	a.	a.	41	100				
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—					
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—												

Table I (contd.).

Aspect Slope	Life- form	Western Downs (mainly wooded) (Cocking gap to River Arun)									West-central Downs (River Arun to River Adur)								
		Extreme W.																	
		E.	E.	N.N.W.	N.	W.	E.	S.	S.	N.	W.	W.N.W.	N.	N.	N.W.	N.	N.	N.	S.E.
		24- 35°	16°	18- 20°	32°	10°	10- 12°	22°			18- 32°	22- 32°	32- 37°	15°	27°	27°	5°		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Gentiana amarella</i>	Th	o.	r.-o.	o.	o.	o.-f.	o.	—	—	o.	—	o.	o.	o.	—	o.	o.	—	—
<i>Habenaria viridis</i>	G	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helianthemum vulgare</i>	Ch	—	—	o.-l.d.	—	l.	—	o.-f.	—	—	—	—	l.	—	—	l.	—	—	—
<i>Hieracium pilosella</i>	H	l.a.	l.a.	f.- l.d.	o.	o.	o.	f.- v.a.	v.a.	o.	f.	f.-a.	l.f.	o.	—	o.-f.	f.-a.	—	l.a.
<i>Hippocrepis comosa</i>	H	—	—	a.-l.d.	—	—	—	—	—	—	—	—	—	—	—	—	l.	—	—
<i>Holcus lanatus</i>	H	—	—	—	—	l.a.	l.	—	—	l.	o., l.	—	l.	l.	—	l.	—	—	o.
<i>Hypericum perforatum</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hypochaeris radicata</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.
<i>Koeleria gracilis</i>	H	f.	—	o.-f.	o.	o.-f.	f.-a.	o.-f.	o.-f.	—	f.	l.f.	—	l.	o.	f.	o.-f.	o.	f.
<i>Lathyrus pratensis</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Leontodon autumnalis</i>	H	o.	o.-a.	f.	o.	—	o.	—	—	o.	o.	—	o.	o.	—	o.	—	—	f.
<i>L. hispidus</i>	H	a.	f.-a.	f.-a.	l.a.	f.	f.-a.	v.a.	f.	o.-f.	o.-f.	f.	a.	f.	o.	o.	f.	o.	o.
<i>Leucanthemum vulgare</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	o.	o.	—	—	—	—
<i>Linum angustifolium</i>	Th or H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. catharticum</i>	Th	o.	o.-f.	f.-a.	f.	f.	o.-a.	f.-a.	o.	f.	o.	f.	f.	f.	—	o.-f.	f.-a.	o.	f.
<i>Listera ovata</i>	G	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lolium perenne</i>	H	—	l.	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lotus corniculatus</i>	H	a.	a.	f.	f.	f.-a.	f.	f.-a.	a.	f.	f.	a.	o.	f.	a.	f.	a.	a.	a.
<i>Luzula campestris</i>	H	—	—	—	—	o.	—	—	—	o.	—	—	—	—	—	—	o.	—	—
<i>Medicago lupulina</i>	Th	f.	—	o.	o.	o.-f.	—	o.	—	—	—	—	f.	o.	o.	—	—	—	a.
<i>Myosotis arvensis</i>	Th	l.	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ononis repens</i>	H	l.f.	—	—	—	f., l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Opbrys apifera</i>	G	—	—	—	—	—	r.	o.	—	—	—	—	—	—	—	—	—	—	—
<i>Orchis maculata</i>	G	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. pyramidalis</i>	G.	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Origanum vulgare</i>	H	l.	—	—	—	l.	l.	o.	—	—	—	—	—	—	—	—	—	—	l.
<i>Phleum pratense</i>	H	l.f.	o.	—	o.	o.	o.	—	—	o.	o.	o.	—	—	—	—	o.	—	f.
<i>Phyteuma orbiculare</i>	H	—	l.	o.	—	r.	o.	o., l.f.	o.	—	—	o.	r.	—	o.	—	o.	f.	—
<i>Picris hieracioides</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.
<i>Pimpinella saxifraga</i>	H	f.	o.	o.	o.	f.	o.	o.	—	—	o.	o.	o.	o.	f.	—	o.	f.	o.
<i>Plantago lanceolata</i>	H	a.	f.-a.	f.	f.	v.a.	f.	f.	o.	f.	f.	f.	a.	f.	f.	a.	a.	a.	f.-a.
<i>P. media</i>	H	o.	l.	o., l.	—	—	o.-f.	o.-f.	o.	l.	o.	o.	f.	o.	o.	r.	—	—	o.
<i>Poa pratensis</i>	G	—	—	—	—	o.	—	—	—	—	l.	—	—	—	o.	—	l.	l.	—
<i>Polygala vulgaris</i>	H	o.	o.	o.	o.	—	f.	f.	—	—	—	o.	—	—	—	o.	f.	—	—
<i>Potentilla anserina</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.f.
<i>P. erecta</i>	H	—	—	—	—	—	r.	l.	—	—	—	—	—	—	—	f.	—	—	—
<i>P. reptans</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.a.
<i>Poterium sanguisorba</i>	H.	a.- l.v.a.	—	f.	a.	o.- l.v.a.	l.a.	v.a.	—	l.	a.	a.	a.	f.-a.	o.- l.f.	a.	v.a.- c.d.	f.	l.a.
<i>Primula veris</i>	H	l.	r.-o.	l.	r.	o.-f.	f.-a.	o., l.	—	—	—	o.	o.	—	o.	—	l.f.	l.	—
<i>Prunella vulgaris</i>	H	o.	o.-f.	o.	o.-f.	—	o.	—	l.	o.	o.	o.	f.	o.	o.	f.	f.	—	f.
<i>Ranunculus acer</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—
<i>R. bulbosus</i>	H	o.	o.	o.	—	a.	o.-f.	f.	o.	—	—	o.	—	—	o.	—	a.	—	o.
<i>R. repens</i>	H	—	r.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhinanthus crista-galli</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Reseda lutea</i>	Th or H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rumex acetosa</i>	H	—	o.	—	o.	o.-l.a.	—	—	—	—	—	—	—	—	o.	—	o.-f.	r.	—
<i>Scabiosa arvensis</i>	H	o.	—	—	—	r.-o.	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>S. columbaria</i>	H	f.	o.	o.	o.	o.	f.-l.a.	—	o.	—	f.	f.	f.	f.	f.	o.	o.	f.	f.
<i>S. succisa</i>	H	o.	l.a.	—	—	—	—	—	—	—	—	—	o.-f.	—	—	—	—	—	—
<i>Senecio campestris</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(Cineraria integrifolia)																			
<i>S. jacobaea</i>	H	r.	o.	—	—	o.	o.	—	—	f.	—	—	—	r.	r.	o.	—	—	—
<i>Sieglingia decumbens</i>	H	—	—	—	—	—	l.	—	—	—	—	—	—	—	—	o.	—	—	—
<i>Sonchus oleraceus</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spiranthes autumnalis</i>	H	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tamus communis</i>	G	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	—
<i>Taraxacum erythrospermum</i>	H	o.	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	o.	—	—
<i>T. officinale</i>	H	o.	—	—	—	o.	—	—	o.	—	—	—	—	—	—	—	—	r.	—
<i>Thesium linophyllum</i> (humifusum)	G	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thymus serpyllum</i>	Ch	a.	a.	a.	f.-a.	l.	o.-l.f.	o.-a.	f.-a.	f.	o.	a.	f.	o.	o.	f.	a.	o.	a.

Table I (contd.).

Eastern Downs																							Occurrences	
East-central Downs (River Adur to River Ouse)											Mount Caburn group east of Lewes				Firle region		Maritime region extreme east					No. of areas	%	
N. 15- 25° 19	N. 30- 32° 20	N. 30- 35° 21	N. 32- 37° 22	N. 37- 40° 23	N. 22- 24° 24	N.N.W. 30° 25	S.S.E. 30° 26	N. 35- 37° 27	N. 30° 28	N. 30° 29	S. 23- 28° 30	N. 23° 31	S. 18- 32° 32	Flat 33	S. 10- 15° 34	N. 30° 35	N. 30- 32° 36	S.E. 20- 24° 37	Flat 38	W. 5° 39	Flat 40			S. 41
—	—	—	o.	o.	o.	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	16	40
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	o.	a.	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	f, l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	76
l.d.	—	—	—	—	—	o.	a-d.	—	—	—	v.a.	f.	l.a.	—	l.a.	l.	l.	l.a.	—	v.a.	—	l.a.	14	35
o.	l.a.	o.	—	l.	l.	—	—	l.a.	a.	l.a.	—	l.	—	—	l.	o, l.a.	—	—	—	—	—	—	19	47
—	—	—	—	l.	—	—	—	l.	—	—	—	l.	—	—	—	—	l.f.	—	—	—	—	—	4	10
f-a.	f-a.	o.	a.	l.	f.	o.	—	l.a.	o.	a.	—	—	a.	o-f.	—	f.	l.f.	f.	f.	f.	o.	f-a.	34	85
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
o.	o.	l.	f.	a.	f.	—	a.	—	l.a.	—	o-f.	a.	f.	—	—	a.	f-l.a.	f.	f.	—	—	—	12	30
—	—	—	o.	—	—	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	33	80
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	17
o-f.	f.	l.	f.	f.	f.	o-l.a.	f-a.	o.	—	f-a.	f-a.	o.	a.	v.a.	v.a.	f.	f.	f.	—	f.	a.	r-o.	1	2
—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	93
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
f.	f.	o.	o.	a.	o-f.	o.	—	o.	—	a.	—	o.	o.	f.	—	f.	o.	a.	a.	f.	a.	f.	37	90
f.	—	o.	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	f.	—	f.	—	—	—	—	—	—	—	f.	—	l.f.	—	—	—	o.	o.	o.	—	o.	—	20	50
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	17
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	32
a.	f.	o.	f.	a.	f.	o-f.	o.	—	—	r.	o.	f.	o.	o.	—	f.	l.	o.	o.	—	—	—	28	70
r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10
f.	a.	o.	a.	f.	o-f.	f.	o-f.	a.	a.	o.	o.	f.	l.a.	f.	f-a.	—	f.	a.	f.	o.	—	—	34	85
f.	a.	f.	f.	o.	f.	o.	f.	a.	a.	f-a.	f-a.	f.	f-a.	f-a.	f.	f.	f.	a.	a.	f.	f.	f.	41	100
l.f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	71
o.	—	v.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	27
l.f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	54
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
v.a.-cd.	a.	v.a.	f.	f.	a.	a-l.d.	a.	l.v.a.	a.	a.	a-l.v.a.	v.a.	a.	v.a.	v.a.	f.	l.a.	a.	v.a.	a.	a.	v.a.-cd.	39	95
o-l.a.	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	60
—	o.	f.	—	f.	f.	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	65
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	65
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
o.	o.	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	42
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12
o.	a.	o.	a.	f.	a.	o.	—	l.a.	l.a.	f.	f.	f.	f.	o.	o.	f.	f.	o.	o.	o.	—	o.	37	90
l.	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	32
o-f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	37
—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	17
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
o.	a.	—	a.	a.	f.	o.	f.	l.	l.	f.	f.	l.	l.a.	f.	o-f.	f.	l.a.	l.	v.a.	f.	a.	o.	40	98

Table I (contd.).

Aspect Slope	Life- form	Western Downs (mainly wooded) (Cocking gap to River Arun)										West-central Downs (River Arun to River Adur)									
		Extreme W.																			
		E. 24-35°	E. 16°	N.N.W. 18-20°	N. 32°	W. 10°	E. 10-12°	S. 22°	S.	N.	W.	W.N.W.	N. 18-32°	N. 22-32°	N.W. 32-37°	N. 15°	N. 27°	N. 27°	S.E. 5°		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
<i>Tragopogon minus</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—		
<i>Trifolium pratense</i>	H	f.-l.a.	o.-f.	—	o.	o.	o.	—	o.	o.	o.	o.	f.-a.	f.	f.	o.	o.	a.	—		
<i>T. procumbens</i>	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.		
<i>T. repens</i>	H	—	o.-l.a.	—	—	o.	—	—	—	o.	o.	—	—	—	—	f.	—	o.	—		
<i>Trisetum flavescens</i>	H	f.	—	o.	o.	f.	f.	—	f.	f.	o.	—	f.	a.	o.-f.	f.	f.	v.a.	—		
<i>Tussilago farfara</i>	G	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Verbena officinalis</i>	H	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Veronica chamaedrys</i>	Ch	—	o.	—	o.	l.	o.	—	l.	—	—	—	o.	o.	o.	o.	—	l.	—		
<i>V. officinalis</i>	Ch	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	l.	—	r.	—		
<i>Vicia cracca</i>	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.-f.	—	—		
<i>Viola hirta</i>	H	l.	f. l.a.	l.	—	—	l.	—	—	—	l.f.	—	o.	—	f.	l.f.	—	—	—		
<i>V. riviniana</i>	H	—	o.	—	f.	—	—	—	—	—	—	—	—	—	o.	r.	—	—	—		
Flowering plants 126																					
BRYOPHYTES																					
<i>Barbula cylindrica</i>	—	—	—	—	f.	f.	l.a.	o.	f.	a.	f.	a.	a.	a.	f.	a.	a.	l.a.	—		
<i>Brachythecium purum</i>	—	a.	a.	a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Campothecium lutescens</i>	—	f.	a.	a.	o.	o.	—	—	v.a.	—	—	a.	f.	—	—	a.	—	v.a.	—		
<i>Dicranum scoparium</i>	—	f.-a.	a.	l.a.	v.a.	—	—	o.	—	—	—	l.	—	f.	—	a.	a.	—	—		
<i>Fissidens adiantoides</i>	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>F. taxifolius</i>	—	o.	—	—	—	o.	o.-f.	—	f.	o.	—	—	—	—	—	o.	o.	—	—		
<i>Hylacomium splendens</i>	—	—	l.d.	—	v.a.	—	—	—	—	—	—	—	l.a.	l.a.	v.a.	v.a.	l.f.	—	—		
<i>H. squarrosum</i>	—	o.	a.-l.d.	l.a.	f.-a.	o.	—	—	—	l.a.	o.	—	a.	o.	o.	l.f.	l.a.	—	a.		
<i>H. triquetrum</i>	—	l.a.	a.	l.a.	a.	—	—	—	—	f.	—	l.f.	l.a.	a.	v.a.	l.a.	a.	l.a.	—		
<i>Hypnum chrysophyllum</i>	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>H. cupressiforme var. elatum</i>	—	o.	f.	l.	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>H. cuspidatum</i>	—	l.f.	o.	—	o.	f.	f.	—	—	—	—	l.a.	—	f.	o.	—	—	f.	—		
<i>H. molluscum</i>	—	—	f.-a.	f.	o.-f.	—	—	—	—	—	—	—	—	—	—	—	f.	—	—		
<i>Mnium undulatum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Neckera crispa</i>	—	—	o.-f.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Rhacomitrium lanuginosum</i>	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Seligeria calcarea</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Thuidium abietinum</i>	—	—	f.	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>T. tamariscinum</i>	—	—	o.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Frullania tamarisci</i>	—	—	o.-l.a.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Scapania nemorosa</i>	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
Bryophytes 21																					
LICHENS																					
<i>Cladonia fimbriata</i>	—	—	l.a.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>C. silvatica</i>	—	l.f.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Collenia sp.</i>	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Peltigera sp.</i>	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
Lichens 4																					
Total species 151		74	68	50	52	64	56	38	29	36	41	45	45	44	46	51	58	39	58		
SOILS																					
Depth of sample	—	1-4"	—	0-2"	—	0-5"	—	—	—	0-2"	—	—	0-3"	—	0-2"	0-2"	0-2"	0-2"	—		
Hydrogen-ion concentration (pH) †	—	7.4	—	7.4	—	6.9	—	—	—	7.2	—	—	7.8	—	7.6	7.2	6.9	6.5	—		
Water loss at 100° C.	—	5.5	—	6.2	—	7.4	—	—	—	10.9	—	—	5.4	—	6.2	7.6	7.7	5.8	—		
Loss on ignition (mainly organic matter)	—	20.5	—	25.9	—	32.0	—	—	—	38.2	—	—	17.3	—	28.2	30.6	31.6	24.0	—		
CaO	—	17.4	—	27.4	—	11.1	—	—	—	2.4	—	—	33.7	—	30.2	1.9	21.7	25.7	—		
Lime as CaCO ₃	—	31.1	—	49.0	—	19.8	—	—	—	4.3	—	—	60.1	—	53.9	3.4	38.8	45.9	—		
MgO	—	0.19	—	0.32	—	0.35	—	—	—	0.34	—	—	0.31	—	0.22	0.58	0.29	0.20	—		
K ₂ O	—	0.21	—	0.58	—	0.29	—	—	—	0.36	—	—	0.26	—	0.17	0.34	0.31	0.16	—		

† The pH determinations were made by the electrical method. 5 gr. soil were ground up and shaken with 50 c.c. $\frac{1}{2}$ saturated KCl and filtered.

Table II.

	Chalk Heaths						Heaths	
	A	B	C*	D	E	F	a	b
<i>Achillea millefolium</i>	f.	f.—a.	—	f.	a.	f.	f.	f.
<i>Agrimonia eupatorium</i>	—	—	l.	—	—	—	—	—
<i>Agrostis alba</i>	—	o.	a.	—	—	—	l.a.	f.
<i>A. tenuis</i>	f.	v.a.	l.a.	o.—v.a.	v.a.—d.	f.—l.a.	o.—f.	f.
<i>Aira praecox</i>	—	l.	—	—	—	—	—	—
<i>Anthoxanthum odoratum</i>	—	—	—	f.	l.a.	a.	o.	—
<i>Anthyllis vulneraria</i>	—	—	l.a.	o.	—	o.	—	—
<i>Arenaria serpyllifolia</i>	—	—	—	o.	o.	—	—	—
<i>Asperula cynanchica</i>	o.	o.	o.	a.	f.	o.	—	—
<i>Avena pratensis</i>	—	—	o.	f.	—	—	—	—
<i>A. pubescens</i>	—	l.a.	l.a.	—	—	—	—	—
<i>Bellis perennis</i>	o.	l.f.	o.	f.	f.	l.a.	—	—
<i>Brachypodium pinnatum</i>	—	—	l.d.	—	l.	l.d.	—	l.d.
<i>B. silvaticum</i>	—	l.	l.	—	—	—	l.	—
<i>Briza media</i>	o.	—	—	o.—f.	f.	f.	—	—
<i>Bromus erectus</i>	—	—	l.	—	—	—	—	—
<i>B. mollis</i>	—	—	l.	—	—	—	—	—
<i>Calluna vulgaris</i>	o.	f.	—	a.	o.—f.	f.	l.a.	l.a.
<i>Campanula glomerata</i>	—	—	—	—	—	—	o.	—
<i>C. rotundifolia</i>	f.	a.	—	f.	f.	—	f.	f.
<i>Carex caryophyllea</i>	a.	a.	—	f.	f.	o.	—	o.
<i>C. flacca</i>	a.	l.a.	—	f.	o.	o.—f.	l.a.	r.
<i>C. pilulifera</i>	—	—	—	—	—	—	l.a.	o.
<i>Carlina vulgaris</i>	—	—	o.	—	o.	o.	—	—
<i>Centaurea nigra</i>	—	—	r.	o.	—	—	—	o.
<i>Cerastium vulgatum</i>	—	—	—	o.	f.	—	a.	—
<i>Cirsium acaule</i>	f.—a.	f.	o.	o.	f.	f.—a.	l.a.	—
<i>C. arvense</i>	—	—	o.	—	r.	—	o.	l.
<i>C. lanceolatum</i>	—	—	r.	—	r.	—	—	—
<i>C. palustre</i>	o.	o.	—	—	—	—	o.	o.
<i>Clinopodium vulgare</i>	—	—	—	—	—	—	r.	—
<i>Crepis virens</i>	—	o.	f.	—	—	—	—	—
<i>Cynosurus cristatus</i>	—	—	l.	f.	v.a.	o.	—	—
<i>Dactylis glomerata</i>	—	—	f.—a.	l.	—	f.	o.	—
<i>Daucus carota</i>	—	—	o.	r.	—	l.	—	—
<i>Deschampsia caespitosa</i>	—	—	—	—	l.	o.	—	—
<i>Erica cinerea</i>	—	—	—	—	—	o.	a.—d.	d.
<i>Euphrasia nemorosa</i>	o.	o.	o.	—	—	f.	o.	—
<i>Festuca ovina</i>	a.	v.a.—d.	a.	a.	v.a.	a.	a.	f.—l.a.
<i>Filipendula hexapetala</i>	—	—	—	a.	—	o.	—	l.
<i>Fragaria vesca</i>	l.	—	—	o.	—	—	l.f.	—
<i>Galium mollugo</i>	o.	—	—	—	—	—	—	—
<i>G. saxatile</i>	—	o.—f.	—	—	—	—	—	o.
<i>G. verum</i>	f.	o.—f.	l.	f.	—	o.	f.	—
<i>Gentiana amarella</i>	o.	—	—	o.	—	—	—	—
<i>Helianthemum vulgare</i>	—	—	—	—	—	—	l.	—
<i>Hieracium pilosella</i>	a.	f.	l.v.a.	f.	l.a.	—	l.	—
<i>Hippocrepis comosa</i>	—	—	—	f.	—	—	—	—
<i>Holcus lanatus</i>	l.	l.	l.	l.a.	l.v.a.	o.	l.f.	—
<i>Hypericum perforatum</i>	—	—	—	—	—	—	l.f.	—
<i>H. pulchrum</i>	—	—	—	—	—	—	o.	o.
<i>Hypochaeris radicata</i>	—	—	—	—	—	—	o.—f.	r.
<i>Inula squarrosa</i>	—	—	o.	—	—	—	o.	—
<i>Koeleria gracilis</i>	—	—	f.	f.	—	—	—	—
<i>Leontodon autumnalis</i>	f.	f.	o.	f.	o.	f.	o.	—
<i>L. hispidus</i>	f.	f.	o.	l.a.	—	—	o.	—
<i>Linaria vulgaris</i>	—	—	r.	—	—	—	—	—
<i>Linum catharticum</i>	f.	o.	a.	a.	o.	f.	—	—
<i>Lotus corniculatus</i>	a.	a.	a.	o.	a.	a.	a.	f.
<i>Luzula campestris</i>	o.	f.	—	—	o.	—	—	—
<i>Medicago lupulina</i>	—	—	a.	f.	—	o.	—	—
<i>Origanum vulgare</i>	—	—	l.	—	—	—	—	—
<i>Phleum pratense</i>	o.	—	l.	—	—	—	—	—
<i>Phyteuma orbiculare</i>	—	—	—	o.	—	o.—f.	—	—
<i>Pimpinella saxifraga</i>	—	—	o.	—	o.	o.	o.	o.
<i>Plantago lanceolata</i>	f.—a.	a.	a.	a.	a.	a.	f.	—

* This area is not a chalk heath but is situated on the plateau adjacent to chalk heaths and is included for comparison. Possibly it has been recently ploughed: see the soil analysis.

Table II (contd.).

	Chalk Heaths						Heaths			
	A	B	C*	D	E	F	a	b		
<i>Plantago media</i>	—	—	o.	—	—	—	—	—		
<i>Poa pratensis</i>	—	—	l.a.	—	—	—	—	—		
<i>Polygala vulgaris</i>	—	o.	—	f.	—	o.	—	—		
<i>Potentilla anserina</i>	—	—	l.a.	—	—	—	—	—		
<i>P. erecta</i>	o.	f.	—	o.	—	—	a.	—		
<i>P. reptans</i>	r.	—	—	—	—	—	—	—		
<i>Poterium sanguisorba</i>	l.f.	l.	l.f.	a.	f.—l.a.	a.	l.a.	l.a.		
<i>Prunella vulgaris</i>	o.	o.	f.	o.—f.	f.	—	f.	—		
<i>Ranunculus bulbosus</i>	—	—	f.	o.—f.	o.	o.	—	—		
<i>Rumex acetosa</i>	r.	f.	—	—	f.	o.	o.	o.		
<i>Scabiosa arvensis</i>	—	—	—	—	—	—	o.	—		
<i>S. columbaria</i>	—	—	f.	o.	o.	o.	—	—		
<i>S. succisa</i>	—	—	—	o.	—	—	l.a.	—		
<i>Senecio jacobaea</i>	—	o.	—	—	o.	—	l.	o.		
<i>Sieglingia decumbens</i>	—	—	—	l.a.	—	l.	—	o.		
<i>Silene cucubalus</i>	—	—	o.	—	—	—	—	—		
<i>Stachys (Betonica) officinalis</i>	—	—	—	—	—	—	l.a.	f		
<i>Taraxacum erythrospermum</i>	—	—	—	o.	—	—	—	—		
<i>T. officinale</i>	o.	o.	—	—	—	—	—	—		
<i>Teucrium scorodonia</i>	—	—	—	—	—	—	l.a.	—		
<i>Thymus serpyllum</i>	a.	f.	f.	f.—a.	a.	f.	f.—a.	l.		
<i>Trifolium pratense</i>	—	o.	f.	f.	a.	o.	o.	—		
<i>T. procumbens</i>	—	—	f.	—	—	—	—	—		
<i>T. repens</i>	—	l.a.	o.	a.	v.a.	—	—	—		
<i>Trisetum flavescens</i>	—	—	v.a.—d.	—	f.	o.	—	—		
<i>Ulex nanus (minor)</i>	—	—	—	—	—	—	—	a.		
<i>Valeriana officinalis</i>	—	r.	—	—	—	—	l.f.	—		
<i>Verbena officinalis</i>	—	—	—	l.a.	—	—	—	—		
<i>Veronica chamaedrys</i>	—	o.	—	o.	—	—	o.	—		
<i>V. officinalis</i>	f.	o.	—	l.	—	—	o.	—		
<i>Viola hirta</i>	—	—	—	l.	—	—	l.f.	—		
<i>V. riviniana</i>	o.	l.a.	—	—	—	o.	f.	o.		
MOSSES										
<i>Barbula cylindrica</i>	—	—	—	—	—	—	—	l.		
<i>Brachythecium purum</i>	a.	a.	—	a.	a.	—	a.	a.		
<i>B. rutabulum</i>	—	—	l.	—	—	—	—	—		
<i>Bryum capillare</i>	—	—	—	—	l.	—	—	—		
<i>Camptothecium lutescens</i>	l.a.	f.	—	—	v.a.	o.	—	—		
<i>Catharina undulata</i>	—	l.a.	—	—	—	—	—	—		
<i>Ceratodon purpureus</i>	—	—	—	—	—	—	l.	—		
<i>Dicranum scoparium</i>	v.a.	f.—a.	—	l.a.	l.	l.	f.	—		
<i>Hylacomium splendens</i>	l.	—	—	—	—	—	—	—		
<i>H. squarrosum</i>	f.	l.a.	—	—	f.	o.	—	l.		
<i>H. triquetrum</i>	l.a.	l.a.	—	—	—	o.	—	—		
<i>Hypnum cupressiforme var. elatum</i>	o.	—	—	—	—	—	—	—		
<i>H. cupressiforme var. ericetorum</i>	—	l.a.	—	—	—	—	a.	l.a.		
<i>H. cuspidatum</i>	—	o.	—	—	o.	o.	—	—		
<i>Polytrichum juniperinum</i>	—	—	—	—	—	—	l.a.	—		
<i>Thuidium tamariscinum</i>	—	—	—	—	—	—	f.	—		
LICHENS										
<i>Cladonia fimbriata</i>	l.f.	l.	f.	—	—	f.	o.	—		
<i>C. silvatica</i>	l.a.	—	—	—	—	—	f.	—		
<i>Cladonia sp.</i>	l.a.	—	—	—	—	—	—	—		
<i>Peltigera sp.</i>	—	—	—	—	—	—	o.	—		
Total species	118	45	50	53	53	44	46	57	32	
SOILS										
Depth of sample	0-4"	—	—	0-4"	0-2"	0-4"	—	0-6"	0-8"	
pH	6.9	—	—	7.4	6.0	6.5	—	6.9	5.8	4.6
Water loss of air dry soil at 100° C.	7.2	—	—	3.9	9.0	7.7	—	3.8	5.2	3.0
Loss on ignition (mainly organic)	26.8	—	—	16.1	41.7	24.9	—	17.7	19.5	12.6
CaO	0.97	—	—	6.6	2.0	1.2	—	0.53	0.62	0.51
As CaCO ₃	1.74	—	—	10.0	3.6	2.1	—	0.95	1.11	0.92
MgO	0.21	—	—	0.60	0.62	0.47	—	0.28	0.38	0.39
K ₂ O	0.26	—	—	0.21	0.28	0.25	—	0.26	0.28	0.33

* This area is not a chalk heath but is situated on the plateau adjacent to chalk heaths and is included for comparison. Possibly it has been recently ploughed: see the soil analysis.

on gentle slopes and flat ground, and in the latter conditions become leached and tend to develop chalk heath.

It is noteworthy that the average pH value is nearly the same for all three types of soil, 7.4 to 7.5, though the range is fairly considerable (least in the dark humous soils).

Chalk Heath soils.

	CaO		Loss on ignition		pH	
	Average	Range	Average	Range	Average	Range
4 chalk heath soils	1.18	0.53-2.0	27.8	17.7-41.7	6.6	6.0-6.9

These soils are mostly brown with a relatively high humus content. They show a marked leaching of calcium and a range of pH values between 6 and 7.

Heath soils.

	CaO		Loss on ignition		pH	
	Average	Range	Average	Range	Average	Range
2 heath soils	0.56	0.51-0.62	16.05	12.6-19.5	5.2	4.6-5.8

The two soils examined from heath developed over the chalk were both light brown dry friable loams with a lower mean loss on ignition than the other soils. The average calcium content is lower than in the chalk heath soils and the pH value very markedly lower.

5. SOCIOLOGICAL CONSTITUTION OF CHALK GRASSLAND

In attempting to analyse the status and rôle of the 151 species listed in Table I we may take first the species which occur in 80 to 100 per cent. of the areas examined, i.e. those which possess the highest degree (5) of *constancy* in the terminology of the Zürich-Montpellier school¹, and next those with constancy 4 (60 to 80 per cent. of the areas)—Table III. These two categories contain the kernel of the association, though they do not exhaust the “characteristic” species, some of which are comparatively or even very rare.

The first column of figures gives the “percentage occurrence” of each species, i.e. the percentage of the whole number of areas listed in which it occurs, the second the “average abundance” of the species in the areas where it occurs. The “average abundance” figures have been arrived at by translating the frequency letters used in Table I into numbers, thus: v.a. or d. = 5, a. = 4, f. = 3, o. = 2, r. = 1: l. has been taken as 2, and where l. is prefixed to another symbol the next lower number is taken, thus l.a. = 3: where a range is indicated in the record the mean figure is taken, thus o.—f. = 2.5, o.—a. = 3. The sum of the numbers so obtained for each species is then divided by the number of areas in which the species occurs, and the number thus arrived at is entered to the nearest first decimal place for each species. It is doubtful if the very rough subjective estimates of abundance

¹ **Braun-Blanquet** and **Pavillard**, *Vocabulaire de Sociologie Végétale*, Montpellier, 1922
See notice in *This JOURNAL*, 10, 1922, p. 245.

represented by the frequency letters can properly bear even this small amount of arithmetical treatment, but it is a great convenience to be able to use numbers, so the experiment has been made. It is clear that the treatment often masks some of the facts set out in Table I—not only the actual ranges of abundance, but also the special character of the mode of occurrence of certain species, e.g. *Bromus erectus*, which is nearly always recorded as generally “dominant,” “locally dominant,” or “local,” whereas its “average abundance” arrived at by the plan described is 3, i.e. equivalent to “frequent.” For indications of the actual modes of occurrence of the different species reference must be made to Table I. In the *Vocabulaire* provision is made for recording the kind of (static) distribution (Vertheilungsart) of the species and the extent of ground covered (Deckungsgrad, Arealprozent). These have not been studied in detail by any quantitative method, but the letter l. obviously refers to the former, and d. to the latter, though of course they are only qualitative characterisations. The figures in the third column (“exclusiveness”) will be referred to later (p. 28).

Table III.

Species of constancy 5					Species of constancy 4				
Life-form	Species (16)	Per cent. occurrences	Average abundance	Exclusiveness	Life-form	Species (19)	Per cent. occurrences	Average abundance	Exclusiveness
G	<i>Carex flacca</i>	100	3.6	2	H	<i>Achillea millefolium</i>	76	2.8	2
H	<i>Plantago lanceolata</i>	100	3.3	2	H	<i>Asperula cynanchica</i>	76	2.9	4
H	<i>Cirsium acaule</i>	98	3.4	3	H	<i>Hieracium pilosella</i>	76	3.1	2
Ch	<i>Thymus serpyllum</i>	98	3.0	3	H	<i>Plantago media</i>	74	2.2	3
H	<i>Avena pratensis</i>	95	3.4	3	H	<i>Dactylis glomerata</i>	72	2.9	2
H	<i>Briza media</i>	95	2.9	3	H	<i>Anthoxanthum odoratum</i>	70	3.1	2
H	<i>Festuca ovina</i>	95	4.1	3	H	<i>Phyteuma orbiculare</i>	70	2.3	5
H	<i>Poterium sanguisorba</i>	95	3.9	4	H	<i>Avena pubescens</i>	70	3.2	3
Th	<i>Linum catharticum</i>	93	3.0	3	H	<i>Trisetum flavescens</i>	70	3.0	3
H	<i>Lotus corniculatus</i>	90	3.1	2	H	<i>Campanula rotundifolia</i>	67	2.7	2
H	<i>Scabiosa columbaria</i>	90	2.6	4	H	<i>Centaurea nigra</i>	67	2.4	2
H	<i>Trifolium pratense</i>	88	2.3	2	H	<i>Bellis perennis</i>	65	2.2	2
H	<i>Koeleria gracilis</i>	85	2.7	3	H	<i>Galium verum</i>	65	2.8	2
H	<i>Pimpinella saxifraga</i>	85	2.7	3	H	<i>Prunella vulgaris</i>	65	2.5	2
	<i>Brachythecium purum</i>	82	3.5	2	H	<i>Ranunculus bulbosus</i>	65	2.5	2
H	<i>Leontodon hispidus</i>	80	3.0	2	H	<i>Bromus erectus</i>	62	3.0	4
					Th	<i>Euphrasia nemorosa</i>	60	2.3	2
					H	<i>Primula veris</i>	60	2.0	3
						<i>Hylocomium squarrosum</i>	60	2.9	2
Average abundance of species of constancy 5					Average abundance of species of constancy 4				
3.2					2.7				

It is noticeable that there is good correlation between the constancy and the average abundance (5 and 3.2, 4 and 2.7) of the species of greatest constancy included in these two lists, which means of course that the species occurring in most areas are also on the average most abundant in each area. The species of constancy 5 certainly form in most areas the bulk of the herbage: *Festuca ovina* in the first place, then, very commonly, *Poterium sanguisorba*,

which is often abundantly mixed in the turf throughout the sample. *Brachythecium purum* often forms an almost continuous lower layer, only appearing conspicuously on the surface when the turf is very short. Of the other dicotyledonous herbs *Lotus* and *Thymus* bulk largest of the most ubiquitous and abundant species, *Plantago lanceolata*, *Cirsium acule* and *Leontodon hispidus* with their different habit of growth probably come next, with *Carex flacca*, and then the grasses *Avena pratensis* and *Briza media*. These are impressions, given in default of quantitative analyses of the herbage.

Of the species of constancy 4, *Galium verum* is important locally, sometimes almost rising to co-dominance. The grasses, both those which are specially characteristic of chalk (*Avena pubescens* and *Trisetum*) and those which are ubiquitous on most soils, like *Dactylis* and *Anthoxanthum*, are more local than those in the first list, but sometimes they rise to great abundance and even to dominance. *Bromus erectus* is in a special position. It is very local in the west of the region surveyed, being absent from the majority of the areas, but in the east it is frequently dominant over considerable areas.

Table IV.

Species of constancy 3					Species of constancy 2				
Life-form	Species (16)	Per cent. occurrences	Average abundance	Exclusiveness	Life-form	Species (19)	Per cent. occurrences	Average abundance	Exclusiveness
	<i>Hylocomium triquetrum</i>	56	3.7	2	H	<i>Cynosurus cristatus</i>	37	2.5	2
H	<i>Agrostis alba</i>	54	3.0	2	H	<i>Daucus carota</i>	37	2.3	3
H	<i>Carlina vulgaris</i>	54	2.0	3	H	<i>Senecio jacobaea</i>	37	1.7	2
H	<i>Polygala vulgaris</i>	54	2.1	2	H	<i>Hippocrepis comosa</i>	35	3.0	4
G	<i>Carex caryophylla</i>	52	2.3	2	H	<i>Trifolium repens</i>	35	2.0	2
Th	<i>Medicago lupulina</i>	50	2.4	2	H	<i>Hypnum cuspidatum</i>	35	2.5	2
H	<i>Holcus lanatus</i>	47	2.3	2	H	<i>Deschampsia caespitosa</i>	32	2.6	2
H	<i>Viola hirta</i>	47	2.0	3	H	<i>Phleum pratense</i>	32	2.1	2
Ch	<i>Cerastium vulgatum</i>	45	2.0	2	H	<i>Succisa pratensis</i>	32	2.4	2
H	<i>Galium erectum</i>	45	2.2	3	H	<i>Filipendula hexapetala</i>	32	2.7	4
Ch	<i>Veronica chamaedrys</i>	45	2.2	2	H	<i>Anthyllis vulneraria</i>	30	2.4	4
H	<i>Rumex acetosa</i>	42	2.0	2	H	<i>Leontodon autumnalis</i>	30	2.3	2
	<i>Camptothecium lutescens</i>	42	3.3	3	G	<i>Cirsium arvense</i>	27	2.1	1
	<i>Dicranum scoparium</i>	42	2.9	2	H	<i>Poa pratensis</i>	27	2.3	2
Th	<i>Gentiana amarella</i>	40	2.0	3	H	<i>Viola riviniana</i>	27	1.6	2
	<i>Hylocomium splendens</i>	40	3.6	2		<i>Fissidens taxifolius</i>	27	2.1	2
					H	<i>Arrhenatherum elatius</i>	22	2.3	2
					H	<i>Brachypodium pinnatum</i>	20	2.5	4
					H	<i>Festuca rubra</i>	20	2.9	2
Average abundance of species of constancy 3					Average abundance of species of constancy 2				
2.5					2.3				

The species in Table IV again show a good correlation between constancy and average abundance (3 and 2.5, 2 and 2.3). It is noticeable that the only species of constancy 3 which exceed an average abundance of 3 are the three mosses *Hylocomium triquetrum* (a.a. 3.7), *H. splendens* (a.a. 3.6) and *Camptothecium lutescens* (a.a. 3.3). Of these the first two are abundant or very abundant

on steep northern exposures but not elsewhere. The last is locally very abundant on soils very chalky to the surface.

Hippocrepis comosa is the only species of constancy 2 which shows an average abundance of as much as 3. This is owing to its local abundance, rising to local dominance, forming large clans or societies, in many areas of the eastern half of the region. In the west it is only occasionally met with. *Festuca rubra*, occurring in only 20 per cent. of the areas examined, has an average abundance of 2.9. This again is owing to its local abundance, especially on loose friable soils showing a high pH value (see areas 24 and 41). *Filipendula hexapetala* (a.a. 2.7) also is locally abundant, especially in the east.

All these species, of relatively low constancy and relatively high frequency where they occur, are in one sense or another "characteristic" of the chalk grasslands of the Sussex Downs.

Table V. *Species (81) of constancy 1; i.e. occurring in less than 20 per cent. of the areas (arranged in order of average abundance).*

Life-form	Species	Per cent. occurrences	Average abundance	Exclusive-ness	Life-form	Species	Per cent. occurrences	Average abundance	Exclusive-ness
H	<i>Agrostis tenuis</i>	12	3.0	1		<i>Barbula cylindrica</i>	2	2.0	1
H	<i>Festuca elatior</i>	10	3.0	1		<i>Fissidens adiantoides</i>	2	2.0	1
H	<i>Potentilla reptans</i>	2	3.0	1		<i>Hypnum chrysophyllum</i>	2	2.0	3
	<i>Hypnum molluscum</i>	15	2.9	3		<i>Mnium undulatum</i>	2	2.0	1
	<i>Neckera crispa</i>	15	2.9	3		<i>Rhacomitrium lanuginosum</i>	2	2.0	1
	<i>Frullania tamarisci</i>	7	2.8	1		<i>Thuidium tamariscinum</i>	5	2.0	2
H	<i>Senecio campestris</i>	12	2.7	5		<i>Collema</i> sp.	2	2.0	1
	<i>Cladonia silvatica</i>	7	2.7	2		<i>Peltigera</i> sp.	2	2.0	1
Ch	<i>Helianthemum vulgare</i>	15	2.6	3	G	<i>Ophrys apifera</i>	15	1.9	4
	<i>Thuidium abietinum</i>	5	2.5	3	H	<i>Taraxacum erythrospermum</i>	10	1.9	2
	<i>Scapania nemorosa</i>	5	2.5	1	Ch	<i>Veronica officinalis</i>	17	1.9	1
	<i>Cladonia fimbriata</i>	10	2.5	2	H	<i>Brachypodium silvaticum</i>	12	1.8	1
H	<i>Ononis repens</i>	17	2.4	2	Th	<i>Myosotis arvensis</i>	15	1.8	2
	<i>Hypnum cupressiforme</i>	15	2.3	3	H	<i>Arabis hirsuta</i>	10	1.7	2
	<i>var. elatum</i>				H	<i>Clinopodium vulgare</i>	7	1.7	2
H	<i>Luzula campestris</i>	15	2.2	2	H	<i>Galium mollugo</i>	7	1.7	1
H	<i>Leucanthemum vulgare</i>	17	2.1	2	G	<i>Orchis maculata</i> (type)	7	1.7	3
H	<i>Scabiosa arvensis</i>	12	2.1	2	Th	<i>Rhinathus crista-galli</i>	10	1.7	2
Th	<i>Arenaria serpyllifolia</i>	5	2.0	2	H	<i>Spiranthes autumnalis</i>	7	1.7	2
Th	<i>Blackstonia perfoliata</i>	2	2.0	2	H	<i>Agrimonia eupatorium</i>	7	1.5	2
Th	<i>Bromus mollis</i>	2	2.0	1	Th	<i>Bartsia odontites</i>	5	1.5	1
Ch	<i>Calluna vulgaris</i>	2	2.0	1	H	<i>Caucalis anthriscus</i>	5	1.5	1
H	<i>Campanula glomerata</i>	12	2.0	4	H	<i>Cynoglossum officinale</i>	5	1.5	1
H	<i>Centaurea scabiosa</i>	5	2.0	3	Th	<i>Erythraea centaurium</i>	5	1.5	2
H	<i>Cirsium palustre</i>	5	2.0	2	H	<i>Fragaria vesca</i>	5	1.5	1
Th	<i>Crepis virens</i>	10	2.0	2	Th.H	<i>Linum angustifolium</i>	2	1.5	2
H	<i>Echium vulgare</i>	2	2.0	1	G	<i>Orchis pyramidalis</i>	5	1.5	4
G	<i>Gymnadenia conopsea</i>	7	2.0	3	H	<i>Ranunculus repens</i>	5	1.5	1
H	<i>Hypericum perforatum</i>	10	2.0	2	H	<i>Cirsium lanceolatum</i>	17	1.4	2
H	<i>Hypochaeris radicata</i>	2	2.0	1	H	<i>Taraxacum officinale</i>	17	1.4	1
H	<i>Lolium perenne</i>	5	2.0	2	H	<i>Tragopogon minus</i>	12	1.4	2
H	<i>Origanum vulgare</i>	15	2.0	3	H	<i>Vicia cracca</i>	12	1.4	1
H	<i>Potentilla anserina</i>	2	2.0	1	H	<i>Picris hieracioides</i>	10	1.2	2
H	<i>Potentilla erecta</i>	7	2.0	1	G	<i>Aceras anthropophora</i>	2	1.0	5
Th.H	<i>Reseda lutea</i>	2	2.0	1	H	<i>Anthriscus silvestris</i>	5	1.0	1
H	<i>Sieglingia decumbens</i>	5	2.0	1	G	<i>Habenaria viridis</i>	2	1.0	2
Th	<i>Sonchus oleraceus</i>	15	2.0	1	H	<i>Lathyrus pratensis</i>	2	1.0	1
G	<i>Thesium linophyllum</i>	7	2.0	5	G	<i>Listera ovata</i>	5	1.0	2
Th	<i>Trifolium procumbens</i>	2	2.0	2	H	<i>Ranunculus acer</i>	2	1.0	1
G	<i>Tussilago farfara</i>	2	2.0	1	G	<i>Tamus communis</i>	2	1.0	1
H	<i>Verbena officinalis</i>	2	2.0	1		<i>Seligeria calcarea</i>	2	1.0	1

The species of constancy 1, i.e. those which occur in less than 20 per cent. of the areas listed, number no less than 81 species (64 flowering plants and 17 mosses, liverworts and lichens) or more than half the whole number. Many are casual invaders of the community, others are ubiquitous occasional constituents of grassland, but a few are confined to, or are mainly found in, chalk grassland or at least on soils rich in lime. In this last category we have the orchids *Aceras anthropophora* and *Ophrys apifera*, with *Gymnadenia conopsea*, *Orchis maculata* (type) and *O. pyramidalis*; *Blackstonia perfoliata* (also on clays), *Campanula glomerata*, *Centaurea scabiosa*, *Helianthemum vulgare*, *Reseda lutea*, *Senecio campestris*, *Thesium linophyllum*, and the mosses *Barbula cylindrica*, *Hypnum chrysophyllum*, *H. molluscum*, *Seligeria calcarea*.

Correlation of constancy and average abundance.

Species of constancy	Average abundance
5	3.2
4	2.7
3	2.5
2	2.3
1	1.9

The average abundance of all the species of constancy 1 is 1.9, of the flowering plants alone 1.8, of the bryophytes and lichens alone 2.2. Of the species of constancy 1 with relatively high average abundance we may note *Agrostis tenuis* (a.a. 3) which usually becomes abundant where it occurs on leached surface soils, *Festuca elatior* (a.a. 3), locally dominant on the deeper soils of steep northern slopes, *Potentilla reptans* (a.a. 3), locally abundant as an invader on open soil; *Senecio campestris* (a.a. 2.7), frequent or abundant in several eastern areas where it occurs, and *Helianthemum vulgare* (a.a. 2.6) locally abundant or even dominant here and there on short rabbit-eaten turf. While the first three are not constituents of most chalk grassland, the last two, though local, are very rarely found outside it, the former being of very restricted, the latter of wide distribution in Great Britain.

Exclusiveness. The figures in the last column of Tables III, IV and V constitute an attempt to represent by numbers the degree to which the species are exclusive to the association. According to the practice of the modern Swiss plant-sociologists¹, the figure 5 signifies "almost or quite confined to the association," 4 = "found especially in the association, though also (more rarely) in others," 3 = "preferring on the whole the community to others though also more or less abundant in these," 2 = "indifferent," 1 = "alien to the community."

It is evident that a just characterisation of the exclusiveness of a species in a given community can only be arrived at on the basis of an exhaustive

¹ Braun-Blanquet and Pavillard, *Vocabulaire*, p. 7; also other recent writings of the Zürich school (e.g. Rübel in *This JOURNAL*, 8, p. 18).

knowledge of the constitution of the other communities in which it may occur, and such knowledge does not at present exist. Nevertheless it seems useful to make the attempt. One doubt which appears at the outset is the question whether the semi-natural grasslands of Great Britain developed on limestone formations (such as the carboniferous, oolitic and magnesian) other than the chalk should be reckoned with the chalk grasslands or not. They have so many species and other characters in common that this course might seem correct, but on the other hand a considerable number of the rarer characteristic chalk species are confined to the chalk itself, because the chalk is mainly a formation of the east and south-east of Great Britain, which is also a region of comparatively low rainfall, and thus the dry soil and calcicole continental species which just reach this country are often found upon it and do not extend beyond its area. The highest exclusiveness figure (5) has therefore been confined to those species which, so far as is known, never or very rarely occur in Great Britain except on the chalk.

Only 4 species, *Phyteuma orbiculare*, *Senecio campestris*, *Aceras anthropophora* and *Thesium linophyllum*, receive the highest figure 5¹. It will be noted that while the first-named has a constancy coefficient of 4, occurring in 70 per cent. of the areas listed, the other three have a constancy figure of 1 only, having been met with respectively in 12 per cent., 2 per cent. (one occurrence) and 7 per cent. of the areas. *Phyteuma orbiculare* is confined to the chalk grassland of the southern counties, extending from Wiltshire and Dorset to East Kent, and the region dealt with in this paper coincides with that of its greatest frequency. *Senecio campestris* not only extends from Dorset to Kent, but also northward along the chalk outcrop to Lincolnshire. It is said to occur also in Gloucestershire and Northamptonshire (doubtless in oolitic grassland) and has been recorded also from Anglesea. Nevertheless its extreme rarity off the chalk warrants an exclusiveness figure of 5. The species is also decidedly local on the chalk through most of its range, and the eastern Sussex Downs, included in this survey, are probably the region of its greatest frequency. *Aceras anthropophora* is more eastern in its distribution than the other two species, its centre being Kent and Surrey, and though it is recorded from several places off the chalk², by far the greater number of plants undoubtedly occur in chalk grassland. *Thesium linophyllum* does not extend further north than Norfolk and except for two or three records in the west (Gloucester, Cornwall) it appears to be confined to chalk grassland.

If the whole area of the English chalk grasslands were surveyed there would, of course, be a number of other species not appearing in our survey records to which the exclusiveness figure 5 would belong. These would probably be most numerous on the chalk of Kent and Cambridgeshire.

¹ Whether a given species should receive an exclusiveness figure of 5 or 4 depends upon how the words "almost exclusively" are interpreted: *Aceras anthropophora* for instance might be thought to deserve 4 only.

² e.g. from sand hills in South Wales.

Of the eleven species receiving the exclusiveness figure 4, two have a constancy of 5, two of 4, four of 2, and three of 1.

Poterium sanguisorba is one of the most constant species of chalk and other limestone grassland from Perth and Forfar southwards, and is far more abundant and widespread on these than on any other soils. *Scabiosa columbaria*, while not so abundant, has a very similar distribution. It is perhaps a question whether these two should have 3 rather than 4 as an exclusiveness figure.

Asperula cynanchica has a much more limited distribution, not reaching Scotland, and is much more abundant in chalk grassland than anywhere else, though it occurs on other limestones. *Bromus erectus* has a more restricted distribution still and is a characteristic local chalk dominant, but it gets off the chalk sufficiently to have 4 rather than 5 as an exclusiveness figure.

Hippocrepis comosa is another species of southerly and easterly distribution scarcely reaching Scotland. It is locally very abundant in the chalk grassland. *Filipendula hexapetala* is of somewhat wider distribution but again is mainly concentrated on the chalk. *Anthyllis vulneraria* is much more widely spread in dry pastures than the preceding species but is much commoner on the chalk than elsewhere. *Brachypodium pinnatum* is of quite restricted southern and to some extent eastern and midland distribution. It occurs mainly on the chalk.

There are only three species of constancy 1 to which we have given the exclusiveness figure 4. *Campanula glomerata* is pretty widely distributed on dry pastures throughout Britain, but it is said to be rare in the west, and it is probably far more abundant on the chalk than elsewhere. *Ophrys apifera* has a more restricted distribution, scarcely reaching the extreme north of England and south Scotland. It is apparently strictly confined to limestone soils and by far the greater number of plants probably occur in chalk grassland, where, locally, and in certain years, it is extremely abundant. The distribution of *Orchis pyramidalis* is similar but it is not so strictly confined to limestone. Perhaps it should have an exclusiveness figure of 3 only.

Of the remaining species of constancy 1 a few are of some interest in relation to chalk grassland. *Lathyrus pratensis* was met with in one area and *Vicia cracca* in four established in the grassland. The latter, though its usual habitat is hedges and wood-edges may almost be considered an occasional constituent of chalk grassland. *Sonchus oleraceus* was met with in 5 areas as a colonist. *Tamus communis* is of course a wood-edge, and *Fragaria vesca* a woodland plant, the latter not very infrequently occurring in chalk grassland. *Tussilago farfara* is apparently a pioneer of loose chalk soils¹ which may remain for a time after a turf is established, though it does not flourish. *Cirsium palustre* (like *Agrostis alba* and *Carex flacca*) belongs to the numerous category of species that occur either on wet soils or on dry soils very rich in lime.

¹ See Tansley and Adamson. "The Chalk Grasslands of the Hampshire-Sussex border." This JOURNAL, 13, pp. 180-183.

Twenty-eight species in all (eight out of the sixteen which have a constancy figure of 5) are marked as specially abundant in chalk grassland (excl. 3), sixty-nine species, or more than one-third of the whole list, as "indifferent" (excl. 2), and thirty-eight (none of which except *Cirsium arvense* rises above constancy 1) as "alien."

While there are thus large indifferent and alien elements (the latter due to the proximity of most of the Downs grassland to cultivated soil), comprising indeed more than two-thirds of the whole list of species, the association is, nevertheless, quite well characterised, according to the standards of the Swiss phytogeographers, by the 4 species of exclusiveness 5, the 11 of excl. 4 and the 28 of excl. 3, a total of 43 or 29 per cent. of the whole belonging to one of the three higher grades of exclusiveness. Of the 35 species of constancy 5 and 4, 17 or practically half belong to one of these three higher grades.

Life forms. Only 4 of Raunkiaer's life forms are represented in the list: chamaephytes, hemicryptophytes, geophytes and therophytes.

	Whole list of flowering plants		Species of constancy 5 and 4	
	No. of species	%	No. of species	%
Ch	6	5	1	3
H	91	72	29	88
G	13	10	1	3
Th	16	13	2	6

The preponderance of hemicryptophytes, very marked in the whole list of flowering plants, is even more overwhelming in the species of the two highest degrees of constancy which form the kernel of the vegetation. The other characteristic life form is the geophyte, to which nearly all the orchids belong, but which is not a type showing a high degree of constancy in this association.

It is hoped that this attempt to employ the methods of the Zürich school for the characterisation of this well-marked association and its species may have enabled a clearer picture to be formed of the floristic characters and composition of chalk grassland. It seems to us, however, that the ideal description and characterisation is only to be obtained by further study which will enable the species to be arranged in small, biologically homogeneous groups, rather of the nature of the *synusiae* of Gams¹, which can be characterised and classified in relation to (1) their ecological requirements, (2) the part they play in the economy of the association and its successional phases. By this means a much needed link may be found between the autecology of the species and the vegetational characters of the community.

6. STATUS OF CHALK GRASSLAND

It is obvious that the great bulk of the English chalk grassland is a community fixed and to some extent modified by continuous grazing. No special attention was paid to succession in the collection of the data for this paper,

¹ Gams, H. "Prinzipienfragen der Vegetationsforschung." *Vierteljahrsschr. d. Naturf. Ges. in Zürich*, 63, 1918.

the object being rather to collect floristic and soil data over a fairly wide region, but the observations made confirm and extend the conclusions arrived at in the third of these "Studies¹." We may say with confidence that chalk grassland is a phase in the development of vegetation on a chalk soil, and that the mass of it is a biotically determined climax association, its characteristics being fixed by the continuous grazing factor. In Clements's terminology it is of course a *subclimax*—the true climatic climax being beechwood (*Fagetum silvaticae calcareum*², Beechwood on chalk³, Beech consociation of sere 4⁴). With the biotic factor removed, or much diminished in intensity, two lines of development are indicated: (1) by leaching of the surface soil on flat surfaces or gentle slopes, a development to "chalk heath" and possibly heath, marked by the entrance and increasing dominance of *Calluna* and/or *Erica cinerea*, and their associates; (2) through a phase of scrub and ashwood to beechwood⁵. The first line may, however, be overtaken and obliterated by the second, though the details of this part of the development have not been studied.

In the grassland itself we may distinguish a consociation dominated by *Festuca ovina* or an association in which this grass is very prominent, and it is this which forms the basis of the biotic subclimax. On the unleached soils, when grazing is relaxed, an association dominated by meadow grasses is developed, and here heath development is excluded and the sere would doubtless progress to beechwood, though we are again ignorant of the details.

The cost of the soil analyses, which were carried out at the Cambridge University School of Agriculture, was defrayed by a grant from the Royal Society.

¹ Tansley, A. G. and Adamson, R. S. "The Chalk Grasslands of the Hampshire-Sussex Border." This JOURNAL, **13**, pp. 177-223.

² *Types of British Vegetation*, p. 163.

³ Adamson. "The Woodlands of Ditcham Park." This JOURNAL, **9**, p. 120.

⁴ Watt. "Development and Structure of Beech Communities on the Sussex Downs. Part II, Section III," "The Beech Consociation." This JOURNAL, **13**. See especially pp. 43, 63, 65, etc.

⁵ Tansley. "Redevelopment of Woody Vegetation on Chalk Grassland." This JOURNAL, **10**, p. 168. Watt, *ibid.* Part II, Section I. "Preclimax Stages in the Developmental Succession." This JOURNAL, **12**, p. 145.

A SOIL SURVEY OF HINDHEAD COMMON¹

By F. M. HAINES.

(With sixteen Tables and three Figures in the Text.)

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INTRODUCTORY

The present communication deals with the results obtained from soil surveys carried out on Hindhead Common in July 1921, July 1922, and July 1923 together with a few further observations made in April and July 1924. A preliminary investigation on a relatively small number of samples was undertaken by Fritsch and Salisbury in 1914 (unpublished) with a view to elucidating some of the ecological problems of the heath, but since the results obtained shed little light upon the points at issue, it was suggested to the writer that a more general survey should be undertaken.

The area lies on the Hythe beds of the Lower Greensand, the subsoil being composed of stone and sand. The peat at different points is from 1 to 10 inches thick. Below this there are usually 4 to 6 inches of a light sandy soil, light both in texture and colour, overlying a hard sandstone which usually appears from 7 to 16 inches below the surface.

¹ From the Botanical Department, East London College.

In July 1921 and July 1922 systematic surveys were made in which samples were taken at 100 feet intervals along three main transects across the area. Of these three lines two ran at right angles to the base line (cf. Fritsch and Parker (9)), one at the point 4 and one at the point 12, whilst the third or Middle Line ran along the summit of the central ridge as indicated in the accompanying map (Fig. 1). Samples were also taken from various zones of special interest such as areas recently burnt¹, the total number of samples taken amounting to about 270. In 1923 and 1924 the general survey was not repeated but a number of samples were taken from special zones and burnt areas. The analyses consisted in determinations of water content, hygroscopic moisture, humus, acidity, total salts, calcium and nitrates in samples from 2-inch and 9-inch depths at each point, but calcium and nitrates, though investigated throughout in the analyses of the first year, were not followed up in later years as the first year's results were all negative. In a few cases determinations were also made of aluminium and potassium.

PART I. METHODS

Method of sampling. All loose debris and undecomposed remains were first of all scraped from the surface. The upper inch of soil was then removed with a trowel over an area of about 20 square inches (6-inch circle), the soil of the next 2 inches was loosened and mixed and about 50 gm. were then removed and packed in lever-lid tins completely lined by a folding bag of two or three thicknesses of waxed paper. The tin containing the bag and soil was then weighed on the spot to 0.1 gm. on a balance capable of accuracy to 0.01 gm. if necessary. The amount of fresh soil taken was found on unpacking in the laboratory by difference after weighing the tins and packets. The samples were then air-dried in the laboratory until they attained a roughly constant weight which usually required from two to four months. For this purpose they were exposed in open paper trays lightly covered over with paper to prevent the access of dust. The water contents at this stage are recorded in the tables as hygroscopic moisture but are not always given. About 20 gm. from each sample were then placed in tared evaporating basins, weighed and dried to constant mass in an oven at 100–110° C. They were then re-weighed and the fresh and air-dry water contents calculated. For the determination of total salts and acidity extracts were then made by weighing out 5-gram lots (two from each sample) into 100 c.c. beakers and extracting by intermittent shaking for two hours with 20 c.c.

¹ Samples taken on lines were usually taken at points midway between the corners of the survey squares (see map) and are designated in the tables by the title of the line such as 4, 12, or ML (Middle Line) followed by the two numbers or letters between which they were taken. Thus 4 AB 2 signifies that the sample was taken on the 4 line between the points A and B, and at a 2-inch depth; ML 8, 9 and ML 18–19, 9 signify that the samples were taken on the Middle Line at the point 8, 9 inches deep and on the Middle Line between the points 18 and 19 and 9 inches deep respectively.

of conductivity water¹. The cleanliness of the beakers was in all cases checked immediately before use by placing about 50 c.c. of conductivity water in the first of a row of two dozen or so (according to the size of the batch of samples), pouring it into each beaker in turn along the whole row and then ascertaining that its resistance in the conductivity pipette used was over 11,000 ohms. The process was always repeated until the resistance of the washing water that had been in all the beakers in turn became immeasurable on the bridge used (i.e. was over 11,000 ohms). After extraction the extracts were filtered through No. 40 Ashless Whatman filters which were shown to cause only a negligible increase in conductivity in their filtrates, the funnels for filtering being subjected before use to the same test as the beakers. The conductivities of the extracts were then found by means of the ordinary form of conductivity pipette used in conjunction with a bridge and telephone supplied by the Cambridge Scientific Instrument Company and reading direct by dial adjustments to the nearest 10 ohms. Accuracy to the nearest 10 ohms was found to be amply sufficient as it was always well within the ordinary error of sampling, individual 5-gram samples of the same soil often differing by 10–100 ohms, but in all cases the average was taken of the two readings for the two different extracts from the same sample, a third determination being made if necessary in cases of bad agreement. The values recorded in the tables for "Total salts" give the conductivities of the extracts in gemhos.

The acidities were determined electrometrically using a Clark hydrogen electrode, the extracts being run into the electrode vessel immediately from the conductivity pipette. The apparatus, which was capable with rapid working of accuracy to 0.001 volt (0.02 in the pH), was checked before and after every batch of extracts with standard solutions (2*N* H₂SO₄ and 0.1*N* alkali) so as to eliminate any possibility of error through changes in the condition of the electrode or formation of films on its surface or changes in the constants of the calomel electrode. In the 1922 survey (the first in which acidities were determined) a battery of voltameter cells with nickel electrodes and dilute NaOH as electrolyte was used as a source of hydrogen, the latter being subsequently passed over conc. H₂SO₄, through glass-wool filters, over an electrically heated coil of nichrome wire wound in a quartz tube and lastly over stick potash and a further glass-wool filter before entering the electrode vessel. In the later years, however, it was found that a Kipp's apparatus and potash tubes alone could be used as a source of hydrogen without any detriment to the accuracy of the results within the required limits, so this simpler form was substituted. The results with the two forms of generator were checked against one another and found to be identical within the required degree of accuracy and the apparatus has been checked against carefully prepared buffer solutions with the same result.

¹ Perfect wetting of the soil was ensured at the beginning of the extraction by grinding against the sides of the beaker with a thick hard glass rod.

The extracts normally took about five minutes to come to equilibrium, the equilibrium after such time being quite definite and steady, but frequently the time required was less.

In the 1921 and 1922 surveys the solutions were tested further for nitrates with diphenylamine and the residues left after filtering off the extracts were tested for calcium in a Collin's calcimeter. Both of these tests, however, were invariably negative so were not pursued in later years.

When the 5-gm. lots had been withdrawn from the dried sample and their extracts analysed as above, part or the whole of the remainder (about 10–20 gm.) was utilised for the determination of humus. For this purpose the soil was weighed in porcelain basins and heated to redness until further heating no longer produced any change in colour. Heating was discontinued when it became impossible to bring lighter layers to the surface on stirring, the process usually requiring from 4 to 6 hours, after which the basins plus ash were cooled and weighed.

In the determination of potassium and aluminium (when performed) extracts were prepared in conductivity water from the dry ground fine earth and subsequently filtered, added to the filter washings and concentrated. Potassium was estimated by the perchlorate method, being weighed as perchlorate on a Gooch crucible, and aluminium was estimated as Al_2O_3 by the ignition on foil of the hydroxide precipitated by NH_4OH . (Iron was first removed by precipitating $\text{Fe}(\text{OH})_3$ and $\text{Al}(\text{OH})_3$ together, taking up the filtered and washed precipitate in a minimum quantity of HCl , treating with NaOH , diluting, filtering and re-precipitating $\text{Al}(\text{OH})_3$ alone from the filtrate with NH_4OH and NH_4Cl .)

PART II. RESULTS

THE GENERAL SURVEYS OF 1921 AND 1922.

Table I. *The 4 line in 1921.*

Soil	Water content		Humus		Total salts†		Coefficient of humidity		Salts/humus ratio	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
4 XY	1.2	4.4	17.3	1.2	4540	1099	0.07	3.67	262	915
4 YZ	3.0	3.2	10.3	1.6	2380	552	0.29	2.00	231	345
*4 Z A	70.6	8.1	50.5	6.4	7410	2267	1.40	1.27	147	413
*4 A	78.3	2.1	10.8	1.2	2380	766	7.25	1.75	220	638
4 AB	6.2	1.6	9.9	1.0	2856	595	0.63	1.60	288	595
4 BC	18.9	2.0	28.3	0.9	4875	656	0.67	2.22	171	730
4 CD	3.9	2.0	15.4	2.3	4000	1738	0.25	0.87	260	755
4 DE	2.4	1.6	8.1	0.8	2220	837	0.30	2.00	274	105
4 EF	23.5	2.4	72.0	1.0	16670	1183	0.33	2.40	232	1183
4 FG	3.5	1.5	24.1	0.8	3450	800	0.15	1.88	143	1000
4 GH	3.0	2.6	15.1	1.7	3920	1015	0.20	1.53	260	596
4 HI	1.6	2.7	3.7	1.3	1695	953	0.43	2.08	458	732
4 IJ	4.9	9.2	1.7	1.6	1242	1439	2.88	5.75	730	900
4 JK	3.3	7.2	2.9	3.5	1449	1560	1.14	2.06	500	417
4 KL	11.8	11.2	13.2	11.7	3570	2500	0.89	0.96	270	214

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are soils more than half way up the hillsides and are called "tops."

† The total salts are expressed as the conductivity in gemhos of the extract made up as described on p. 34, see text.

Table II. The 4 line in 1922.

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
4 XY	12.9	8.5	6.7	2.2	2320	1430	1.90	3.86	346	650	3.6	3.8
4 YZ	15.4	7.8	5.6	1.8	2500	1148	2.75	4.33	446	638	3.4	3.8
*4 Z 4	59.6	17.7	31.8	2.3	7400	2468	1.87	7.70	233	107	3.2	3.5
*4 4 A	30.3	10.6	11.9	2.2	3920	1350	2.52	4.82	330	613	3.2	3.9
4 AB	13.5	6.8	5.6	0.6	2320	793	2.43	11.33	414	1320	3.1	3.6
4 BC	16.6	6.8	36.8	2.2	3030	1340	0.45	3.09	82	610	3.4	4.0
4 CD	20.7	—	8.9	2.9	3920	1072	2.32	—	440	370	3.2	3.6
4 DE	10.8	8.2	4.4	1.5	1722	1753	2.45	5.46	391	1170	3.8	3.5
4 EF	117.6	9.3	67.4	1.1	12980	1000	1.74	8.45	192	909	<2.8	4.1
4 FG	9.2	—	3.3	1.9	1438	1000	2.79	—	435	526	4.1	3.9
4 GH	10.5	9.6	1.6	1.4	1585	1110	6.56	6.86	990	792	3.9	3.9
4 HI	10.8	6.9	4.5	0.5	2350	627	2.40	13.80	522	1254	3.0	4.3
4 IJ	18.6	13.4	4.7	3.0	2896	2220	2.96	4.47	615	740	3.5	3.8
4 JK	13.4	15.2	14.9	2.6	2172	2172	0.90	5.80	155	835	3.9	4.2
4 KL	12.5	16.2	4.6	2.8	2102	2322	2.72	5.79	456	828	3.9	4.0

* See note to Table I.

Table II a. Notes on vegetation in proximity of positions where soil samples were taken in 1921.

- 4 XY (Recently burnt, 1920.) Dom. *Ulex nanus*. *Pteris* present. *Erica cinerea* small plants, 3 in. *Cuscuta* occasional on *Ulex nanus*. Few large clumps *Molinia* and numerous very small tufts. *Epilobium angustifolium* present but not frequent, 1½ ft. high, flowering. Peat, ¾ in. 2 in. dark soil. Sandstone 6-9 in. deep.
- 4 YZ (Recently burnt, 1920.) Dom. *Pteris*. *Ulex nanus* almost as abundant as *Pteris*. *Pteris* often 1-1½ ft. high. About one-third of the ground still bare. *Erica cinerea* almost all small plants about 9 in. or 1 ft. apart. *Cuscuta* occasional on *Ulex*. *Molinia* absent. Peat, ¾ in. 2 in. dark soil. Sandstone 1 ft. below surface.
- 4 Z 4 Dom. *Pteris*. *Vaccinium myrtillus* abundant, 1 ft. *Rubus* occasional bushes. *Ulex europaeus* to 30 ft. *Molinia* tufts fairly numerous. *Calluna* frequent. *Erica cinerea* less abundant. *Erica tetralix* present but not frequent. Dom. grass, *Nardus*. Dark soil 2½-3 in.
- 4 4 A Half way up slope. *Erica cinerea* and *Calluna* equally frequent. Average height of vegetation 1 ft. *Calluna* 2 ft. *Pteris* frequent, to 2½ ft.
- 4 AB Average *Calluna-Ulex-Erica*. *Betula* occasional. *Pinus* occasional. Average height of vegetation 10 in. *Calluna* 15 in. *Pteris* infrequent, to 1½ ft.
- 4 BC *Calluna-Ulex-Erica*. Less dense than at 4 AB, few bare patches. Average height of vegetation about 1 ft. *Calluna* rarely above 1 ft. except in hollows. *Pteris* infrequent, mainly about 1 ft., occasionally to 1½ ft. *Betula* and *Pinus* occasional. *Vaccinium myrtillus* occasional, to 5 in. Peat, 2½ in.
- 4 CD *Calluna-Ulex-Erica*. Number of bare patches. Average height of vegetation, 9-10 in. *Pteris* infrequent, mainly poor, about 1 ft. *Ulex nanus* 3 in. *Erica* 7-8 in. *Calluna* 9-10 in. *Betula* and *Pinus* absent.
- 4 DE As CD (above). *Pteris* nearly absent. *Pinus* occasional. *Cladonia* sp. frequent. Peat, 1 in.
- 4 EF Very thick vegetation, no bare patches. Dom. *Calluna*, to 2 ft. 6 in. *Erica cinerea* to 18 in. *Ulex nanus* less frequent than at DE and CD. *Festuca ovina* abundant. *Vaccinium myrtillus* very abundant, 8-9 in. high. *Pteris* frequent, to 2 ft. 6 in. *Pinus* occasional, to 5 ft. *Hypnum* sp. frequent. *Dicranum* on paths. *Usnea* sp. present, also *Parmelia physodes* frequent on dead *Calluna*. Peat, 4 in.
- 4 FG Vegetation sparse with bare patches. *Calluna-Ulex-Erica*. *Calluna* to 12 in. *Ulex* to 7 in. *Erica* to 8 in. *Ulex europaeus* occasional, 3-4 ft. *Pteris* sparse, 18 in. to 2 ft. *Vaccinium* to 4 in. *Rubus* occasional. *Festuca ovina* infrequent, also *Molinia* and *Deschampsia*. Peat, under 1 in.
- 4 GH *Calluna-Ulex-Erica* with bare patches. *Calluna* to 1 ft. *Ulex* to 4 in. *Erica cinerea* to 7-8 in. *Pteris* infrequent, to 1½ ft. Peat, ½ in.
- 4 HI As GH but more *Pteris*, to 18 in. Little *Molinia*. Generally vegetation very poor. Soil stony. No peat.
- 4 IJ Dom. *Calluna* to 3 ft. Vegetation very thick. *Erica* to 2 ft. No *Ulex*. *Molinia* tufts frequent. Small *Betula* occasional. No *Pteris*, except on sandy bare patches.
- 4 JK Vegetation tall, alternating with a number of bare patches. *Calluna* to 15 in. *Erica* equally frequent, 15 in. *Molinia* tufts frequent, 2-3 ft. *Pinus* occasional. *Betula* present. Very little humus.
- 4 KL Freshly burnt. Only *Molinia* sprouting.

Table III. *The 12 line in 1921.*

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
*12 YZ	15.0	6.2	19.1	1.4	5878	3120	0.78	4.43	308	223
*12 Z 12	16.5	2.2	29.5	2.2	6890	1562	0.56	1.00	234	710
12 12 A	21.5	7.2	8.4	3.5	9530	1923	2.56	2.06	1136	550
12 AB	12.1	2.0	32.8	1.4	6250	1150	0.37	1.43	191	821
12 BC	16.9	—	29.5	2.2	8330	1123	0.57	—	280	510
12 CD	53.5	2.1	12.6	1.0	4250	787	4.25	2.10	338	787
12 DE	2.8	3.2	2.7	0.6	1600	1515	1.03	5.33	592	2530
12 EF	0.4	2.8	16.2	3.0	3126	1905	0.03	0.93	193	635
12 FG	2.8	—	20.6	1.4	4000	763	0.14	—	194	545
12 GH	2.1	7.5	29.1	3.6	5550	1600	0.07	2.08	191	445

* Signifies considered as a valley soil for purposes of the calculation of the figures in Table VII.

Table IV. *The 12 line in 1922.*

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
*YZ	27.0	16.4	9.1	3.2	3445	1920	2.97	5.13	379	600	3.4	3.8
*Z 12	133.5	20.7	92.8	8.4	18150	4250	1.43	2.46	198	506	2.9	4.1
12 A	89.4	26.6	97.9	9.6	10000	4760	0.91	2.77	102	496	2.9	3.1
AB	41.7	—	36.4	—	6666	—	1.15	—	185	—	3.3	—
BC	64.7	8.3	22.0	1.0	5710	1000	2.94	8.30	260	1000	3.2	4.2
CD	26.3	4.6	12.4	1.4	4000	840	2.12	3.29	323	600	3.3	4.7
DE	7.1	21.8	2.6	7.7	1885	3030	2.74	2.84	725	394	3.9	3.2
EF	10.1	7.6	2.3	—	1428	733	4.40	—	620	—	3.8	4.3
FG	18.5	9.5	7.1	3.4	2752	1738	2.60	2.80	388	512	3.5	3.5
GH	41.7	9.5	17.8	2.3	6450	2630	2.34	4.14	362	115	2.9	3.8

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are treated as "tops." Cf. footnote to Table I, p. 37.

Table V. *The Middle Line in 1921.*

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salt/humus ratio	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
ML 0	9.3	11.4	17.7	7.5	4440	2150	0.53	1.52	251	287
ML 6	3.3	1.0	11.0	2.5	2856	631	0.30	0.40	260	252
ML 9	10.3	8.5	24.3	1.7	4540	757	0.42	5.00	187	445
ML 15-16	2.5	2.3	9.3	1.1	3278	1010	0.27	2.09	352	917
ML 17	7.0	1.1	11.0	0.7	2060	400	0.63	1.57	187	571
ML 18-19	2.1	0.9	9.1	1.1	2325	512	0.23	0.81	255	465
*ML 20	6.4	0.5	19.8	1.0	382	453	0.32	0.50	193	453
*ML 20-21	10.1	6.9	9.1	2.4	3918	1515	1.11	2.88	430	631
ML 23	5.4	10.2	10.8	2.0	2000	3030	0.50	5.10	185	1515
ML 26	2.5	2.1	6.3	1.3	1562	1103	0.40	1.62	248	848

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are treated as "tops." Cf. footnote to Table I, p. 37.

*A Soil Survey of Hindhead Common*Table VI. *The Middle Line in 1922.*

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
ML												
0	40.5	23.3	13.6	7.5	5880	3840	2.98	3.11	433	512	3.3	3.7
2	13.8	29.8	3.6	5.7	1940	3330	3.84	5.23	539	594	3.7	4.3
6	10.6	10.6	4.1	1.7	2150	937	2.58	6.23	525	551	3.8	4.3
8	31.3	9.6	11.8	2.8	4340	2125	2.65	3.44	368	758	3.2	3.8
10-11	14.0	1.9	5.6	1.3	2665	800	2.50	1.46	475	615	3.0	4.2
13	9.8	11.3	3.7	3.8	1850	1650	2.65	2.98	500	435	3.7	4.0
15-16	21.9	—	16.0	1.3	5700	1098	1.37	—	356	844	3.1	3.4
17	11.2	5.9	5.1	2.5	2560	1050	2.20	2.36	502	420	3.2	3.8
18-19	27.7	9.3	25.2	3.1	5000	1885	1.10	3.00	198	608	3.3	3.3
*20	39.7	8.5	28.3	3.7	6250	1910	1.40	2.30	221	516	3.3	3.7
*21	92.1	25.6	5.1	4.3	4030	2500	18.10	5.95	790	581	3.8	4.1
22	29.5	102.9	10.1	2.4	3635	1480	2.92	42.90	360	617	3.4	3.3
23	—	8.2	—	6.1	—	1430	—	1.34	—	234	—	3.7
24	14.8	5.7	2.2	0.6	1784	533	6.73	9.50	810	888	3.4	4.0
26	34.8	34.3	16.3	1.9	4540	1665	2.13	18.04	278	876	3.5	4.0

* See note to Table I.

The results of the two general surveys are given in Tables I-VI and will serve to show the leading characteristics. The survey of 1921 was made after a very dry season and that of 1922 after a very wet one, so that differences in water content may be taken to represent practically the extreme conditions of the soil in this respect and must be realised to be due to the different seasonal conditions and not only to differences in the quantity or quality of the humus. The rainfall from Jan.-June recorded at Haslemere was 9.51 inches in 1921¹ and 21.19 inches in 1922¹ but it should be pointed out that in both years the samples were taken after a week of fine weather, so that excess of water content in the wet season is not attributable to rain immediately before sampling but represents as nearly as possible a fair equilibrium condition for a wet season. The samples in the two surveys were taken throughout (except where otherwise stated) at exactly the same points (within a few feet). Some notes are appended to the results of the 1921 survey in Table II a to show the condition of the vegetation at different points along one of the transects at the time of sampling.

In the case of the 4 line for which the notes are given the area from which the first two samples were taken had been recently burnt (about 1920) as indicated in the notes, the rest of the line running across heath about 5-6 years old, while of the 12 line with the exception of the first point, 12 YZ, the greater part lay on heath which was more than 15 years old. The rise and fall of the land along these lines can be realised from the contours on the map and also from Fig. 2, but the effect of varying height of slope and topographical position will be dealt with fully later.

The main characteristic of the soils in general, as will be seen at a glance from Tables II, IV and VI, is their very high degree of acidity, in view of which it is scarcely surprising that it was found to be impossible to demonstrate the presence of nitrates by means of diphenylamine and less still that

¹ Average for last 35 years, Jan. to June, 15.15 inches.

no calcium could be demonstrated with the Collin's calcimeter in any of the samples. No trace of nitrates could be detected in any of the extracts tested in the dilution stated although the reagent was shown to be sensitive to a solution of KNO_3 containing 1 part in 500,000¹. That no nitrification took place in such acid soils was concluded as early as 1884 by Deherain (7) and in 1892 by Warrington (27), and Lipman and Wank (20) more recently, working on surface soils from the deltas of the San Joaquin and Sacramento rivers, found the peat of practically no value as a source of available nitrogen whether untreated or treated with steam and acid under pressure. Bryan (3) also finds that even the more resistant nitrogen bacteria such as those of the Soya bean are killed at an acidity of 3.5–3.9. On the other hand Fred and Davenport (8) find a critical pH of 3.3 for the Soya bean organism and a pH as low as 3.1 for that of *Lupinus* roots. Noyes and Conner (22) found that some nitrification took place in acid soils though the activity was increased by the addition of CaCO_3 and disappeared if the soil were left for a period fully saturated. Nitrification and nitrates have also been recorded in acid soils by Abbot, Conner and Smalley (1), Hall, Miller and Gim-mingham (11), Houzeau (13), Petit (23), Temple (26), and White (29), but in the present cases only minute traces could be detected and it seems likely that the explanation lies in the high degree of acidity².

For calcium in one or two cases an alternative method was applied, the soil being treated with dilute HCl and the evolved CO_2 being carried by a stream of CO_2 -free air drawn through the apparatus into standard alkali which was subsequently titrated against standard acid first with phenolphthalein and secondly with methyl orange. The method showed that even 10-gram samples contained no detectable quantity of calcium, the two titrations giving identical results. The calcium content of these soils is therefore extremely low throughout—a fact which accords well with what appears now to be generally accepted concerning the association of calcium deficiency and the characteristic symptoms of “sourness” which are exhibited by these soils. In the present case, however, it may be pointed out that the degree of acidity alone appears amply sufficient to explain these characters without calling in basic ratios to explain the facts.

The mean values of the pH values of the extracts containing 5 gm. soil to 20 c.c. water for all soils taken from areas of the average *Calluna-Ulex nanus-Erica* association were found to be 3.42 for the 2-inch depths and 3.9 for the 9-inch depths, the numbers being based on 38 and 39 samples respectively. The range of pH for 9-inch depths is from 4.7 to 3.1, but very few samples fall outside the range 4.3–3.5, only one sample having a pH

¹ The nitrate reaction could, however, just be detected in some of the soils with an extract of three times the stated strength, from which it appears that the nitrate content (as $\text{KN}(\text{O})_3$) is of the order .00027 per cent.

² The nature of some of the nitrogenous compounds which are present in peat is dealt with by S. L. Jodidi (17) and (18) and by C. S. Robinson (24).

above this upper limit and only a few isolated cases having a more acid lower limit than 3.5, this occurring where there happens to be more than 9 inches of peat. The range for 2-inch depths is from 3.9 to 2.3 but relatively few fall outside the range 3.0–3.6. Thus there is very considerable variation in the acidity even at fairly closely situated points, for which reason it was not considered necessary to record the acidities to more than one place of decimals. The 2-inch samples are almost invariably more acid than the corresponding 9-inch samples, as would be expected from their usually far greater content of organic matter, the 9-inch ones usually coming from a layer of light sandy soil immediately overlying the sandstone. Such a decrease in acidity in sandy soil below peat has also been found by Wherry (28) in the Middle Atlantic States and by Pierson Kelley (19) working on woodland soils from Chester County, Pennsylvania, who found an increase to 15 cm. below the surface and subsequently a decrease. The only exceptions to this rule of lower acidity at the 9-inch depths are found on bare, exposed gravel patches (cf. Fritsch and Parker (9)), which are still uncolonised and possess practically no humus (e.g. less than 1.5 per cent.).

In view of the fact that the acidities as determined by the electrical method and here recorded are of an exceptionally high order it appeared advisable to obtain additional confirmatory evidence of the presence of so large a quantity of acid by some alternative method. In some ten or so representative cases 10-gram lots of soil were accordingly weighed out, extracted with an excess of distilled water and the total titratable acids determined by titration of the extracts with phenolphthalein and $N/6.5644$ NaOH. The results showed that the range of acidity in terms of normality of the ordinary 5 gm. : 20 c.c. extracts used would be from $N \times 0.761 \times 10^{-3}$ in the case of a soil that had been burnt within the last few years to $N \times 9.13 \times 10^{-3}$ in a *Molinia* zone rich in humus. In all the cases taken the acidity by titration was somewhat greater than that found electrometrically. This might be expected considering the probably very weak nature of the acids concerned. In one case in a soil from 3–4 XY the agreement was as close as 3.1 by electrometric determination and a normality of $N \times 1.065 \times 10^{-3}$ by titration which (assuming complete dissociation) would correspond to a pH of 2.96, but in most cases the difference was greater.

The mean value as determined by titration on this relatively small number of samples is about $N \times 1.49 \times 10^{-3}$ and it is interesting to note that the figure is of the same order as certain values recorded by H. Jeffreys (15) for "strongly acid" water from Wannister bog for which he gives the acidity determined by the same method as $N \times 13.2 \times 10^{-4}$. The acidities are of a somewhat remarkable order, but when it is recalled that Olof Arrhenius (2) found that the rates of germination of ordinary crop plants such as barley, corn, cotton and wheat were only reduced respectively to about 1/2, 1/2, 1/3 and 1/6 of the normal rates in neutral solution when

grown on a soil made artificially so acid that an extract of 10 gm.:50 c.c. water (approximately the same concentration as that used by the writer) showed a pH of 3, it becomes a little more believable that *Erica* and *Calluna* and their associates can permanently tolerate such hydrogen-ion concentrations as 2.3 as here seems to be the case, but fixation of nitrogen, which must be carried on by the fungal endophytes of these plants, does not appear yet to have been demonstrated in such circumstances. It has been noted by Healy and Karraker (12), however, also using the Clark hydrogen electrode, that air-dried soils showed a slightly greater acidity than fresh soil, so conditions in the field may not be so acute. On the other hand it has been stated by Conner (6) that moist soils show a loss in acidity on air drying.

Lastly a single acidity determination was made for the sake of additional evidence on an odd sample from near 3 Y by the sugar inversion method described in *Soil Science*, 15, 2, by Parker and Bryan. The result showed an inversion of .909 gm. sugar which, if one extrapolate a curve to their figures for more acid ranges, appears to correspond with a pH of about 3.5. A soil from this region in the previous year's survey gave 3.6 electrometrically.

Turning now to the question of the concentrations of total salts it will be seen that they average round a value of 4200 for the 2-inch depths and about 1200 for the 9-inch depths. These results are expressed as the conductivity in gemhos of the 5 gm. : 20 c.c. extracts in the particular conductivity pipette used. The pipette was standardised by finding in it the conductivity of a $N/100$ solution of KCl, such a solution having a resistance of 177 ohms and a conductivity therefore of 5650 gemhos. Thus the values given in the tables can be obtained in terms of $N/100$ KCl by dividing by 5650. An average sample of garden soil estimated in the same pipette showed a conductivity of 2600 gemhos so that it will be seen immediately by comparison that the heath soils can in no way be said to be particularly poor in their content of electrolytes but rather the reverse.

It will be seen from Tables I-VI and also from Fig. 2 that the total salts of the 2-inch depths, as likewise the water contents, run in general more or less parallel with the humus content. If the two sets of tables (i.e. I, III and V with II, IV and VI) be compared, however, apparent anomalies will be seen to occur where the alterations in total salts, etc. from one year to the next do not run parallel with those in humus as might be expected. Such is the case for instance in the first three points on the 4 line where the line runs down a recently burnt slope but these are special points which will be dealt with later under the effects of burning. In general the acidity, conductivity and water content run closely parallel with the humus content in the sense that would be expected. This is well illustrated in Fig. 2 which shows the variations in humus, water content, total salts and pH along the 4, 12 and Middle lines according to the 1922 survey. The thick lines at the base of the graphs

represent the rise and fall of the ground and their thicknesses represent the approximate heights of the vegetation at different points. Continuous lines all refer to 2-inch depths and dotted lines to 9-inch depths. In the lower graphs the thick lines (both continuous and dotted) give the percentages of humus and the thin lines water contents, in the upper the thick lines give the salt contents and the thin the acidities. The following general rules will be noticed: 2-inch humus contents run above 9-inch humus contents (i.e. thick continuous lines above thick dots in lower graphs); 2-inch water content is greater than 9-inch water content unless the humus percentages happen to be equal or the position is deep in a valley (e.g. in the bottom graphs the thin continuous lines run above the small dots except at 12 DE where the humus contents are equal and at ML 21-22 which is the bottom of a valley). Salt contents run parallel with humus (i.e. thick lines in the upper and lower graphs vary in the same sense) and vary more in the 2-inch depths than in the 9-inch. 2-inch acidities are nearly always greater than 9-inch acidities (thin continuous lines in the top graphs run above the small dotted lines) and 9-inch acidities usually vary in the same sense as the 2-inch. Acidities run parallel with humus contents, a real relation appearing to exist between them as found by Salisbury for woodlands (25), but have no fixed relation with water content, running parallel with water content when the percentage of humus is very large and in the opposite sense when the humus is low and the water content is nevertheless high through a low position on the slope.

The mean value of water soluble potassium in cases where it was determined was found to be 0.054 per cent. and of soluble aluminium 0.1148 per cent. of the dried fine earth.

THE EFFECTS OF WET AND DRY SEASONS.

The effects of wet and dry seasons as brought out by the 1921 and 1922 surveys are shown in Table VII which deals with the variations in water content and the distribution of soluble salts. Sections a-c of the table give the data for the individual lines, the numbers being averages of figures taken from Tables I-VI (see footnote to Table I), and section d shows means for all the tops and all the valleys taken together. It will be seen that in the individual cases the water content for the wet season (1922) may be as much as 600-700 per cent. greater than that for the dry season (Table VII c), the average increases, however, as shown by the figures in section e, being about two-and-a-half and three times the original percentage for 2-inch and 9-inch depths respectively. The coefficient of humidity in the individual cases increases from three to seven times and in the aggregate (section e) becomes about three times the original value, i.e. increases by about 190 per cent. in both depths. It will be seen that the greatest variation in *actual* water contents (VII d) is found in the 9-inch depths on high ground, the next greatest in 2-inch depths on high ground to which the 9-inch valleys

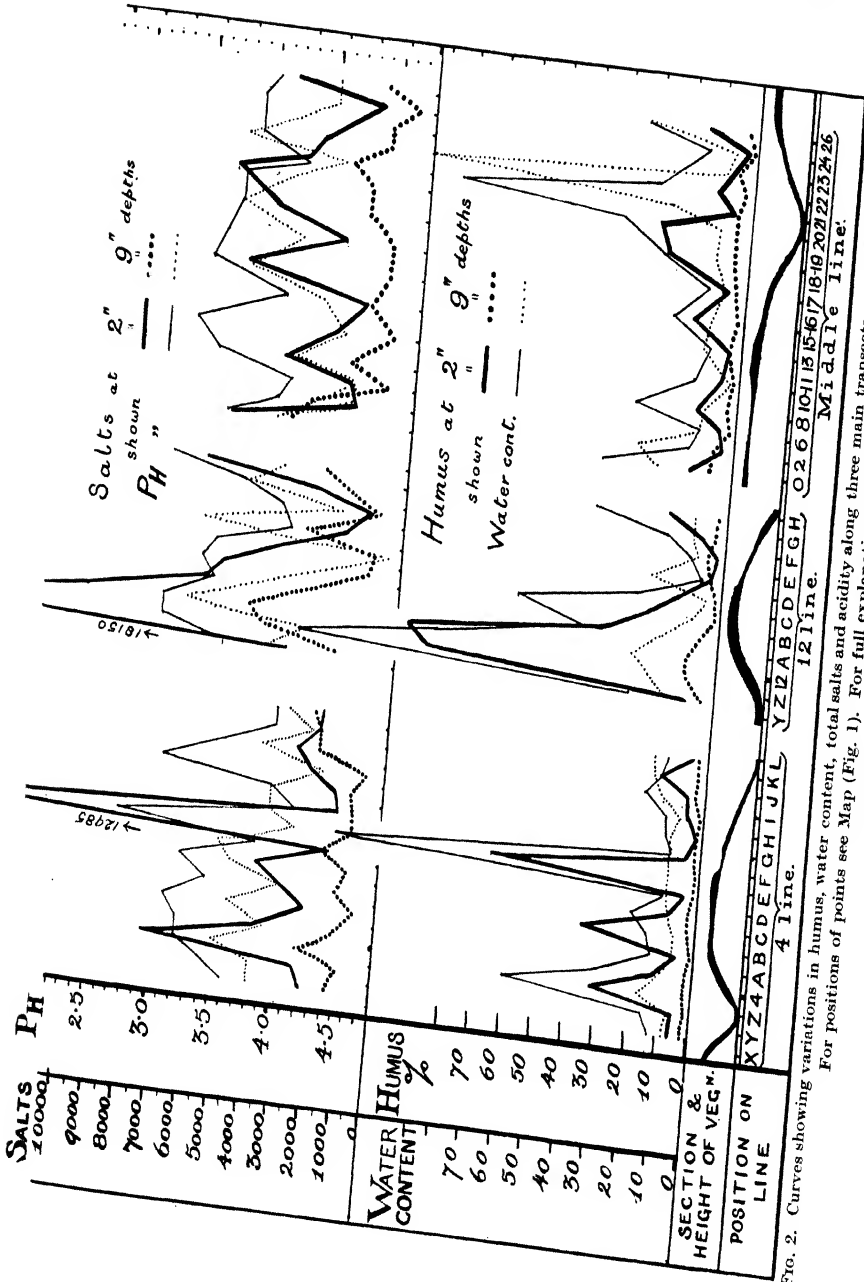


FIG. 2. Curves showing variations in humus, water content, total salts and acidity along three main transects across the area in 1922. For positions of points see Map (Fig. 1). For full explanation see text, pp. 43-44.

run very close and the least variation in the 2-inch depths in the valleys. These points, however, as seen in section d of Table VII, do not probably present the matter quite in its true light, as part of the 4 line which has been included in calculating these means had been burnt only about a year previously to taking the 1921 observations. The values for the water contents and the coefficients of humidity therefore become anomalously high in the valleys in the first (dry) season through the increased facility of drainage down the slopes. The effect of including the values for the 4 line is thus erroneously to reduce the apparent percentage increases in these values from 1921 to 1922 by making the means for 1921 appear much too high. Probably the correct impression is that given in Tables VII d' and e', where the values have been calculated neglecting the anomalous 4 line. From these values it will be seen that the greatest variation in actual water content is really in the 2-inch depths in the valleys, the next greatest in 9-inch depths in the valleys, next in 9-inch tops and least in the 2-inch tops though even here it is increased by 188 per cent. or to nearly three times. The general increase is to about three-and-a-half times in both 2-inch and 9-inch depths but the valleys experience both a higher water content and a greater range in water content than the "tops." (See footnote to Table I, p. 37.)

Probably of greater importance are the variations in water content compared with the amount of humus, or the variations in the coefficient of humidity. These are also recorded in section d and their corrected values ignoring the 4 line in section d'. It will be seen that the humidity is frequently greater on the tops of the slopes than in the valleys, especially in the 9-inch depths in a wet season where it seems to be universally so (VII a, b, c), and in 2-inch depths in both seasons in the case of the very old heath on the 12 line. Otherwise the coefficient of humidity for 2-inch depths is distinctly greater in the valleys (VII a and c), the valleys also experiencing far greater fluctuation in humidity in the different seasons as far as their 2-inch depths are concerned (VII d'), the 9-inch depths fluctuating very much less than the 2-inch and by almost exactly the same amount on the tops and in the valleys. The changes in the coefficient of humidity or "effective wetness" of the soil run closely parallel with those in actual water content in the case of the 2-inch depths but appear to show a less marked relation in the 9-inch depths, a large increase in water content leading here to a relatively small one in the coefficient of humidity (VII d'), especially in the valleys. This result might be expected since in the 2-inch depths the humus must be responsible for holding practically the whole of the water, while in the 9-inch depths where most of the water would, owing to the relative paucity in humus, be held by the sandy mineral fractions of the soil any increase in the amount of humus (as has here taken place) would naturally considerably depress the coefficient. Where the water is originally held mainly by the sand the action of added humus might be compared with

that of a sponge, reducing the "wetness" produced by a given water content, so that the relatively low increase in the 9-inch depth coefficient (80 per cent.) is evidently explained by the incident that a particularly large increase in the percentage of humus happened to take place at this depth during this year, as shown in the last column of section d' of the table.

Table VII. *Mean Values of the water content, humus content, coefficient of humidity, and total salts compared for high- and low-lying ground in dry and wet seasons (1921 and 1922).*

	Position of samples and year	Water content		Humus		Coefficient of humidity		Total salts	
		2"	9"	2"	9"	2"	9"	2"	9"
a	4 line, tops, 1921	5.3	3.6	17.4	1.5	0.6	2.3	2988	1027
	1922	22.5	9.3	13.7	1.8	2.5	6.7	3267	1305
	4 line, valleys, 1921	53.6	6.3	24.8	6.2	3.2	1.3	4440	1978
	1922	34.1	14.5	16.1	2.4	2.5	4.7	4474	2047
b	12 line, tops, 1921	14.0	12.5	15.2	2.1	1.1	2.3	5330	1346
	1922	37.4	12.6	24.8	4.2	2.4	4.0	4858	2103
	12 line, valleys, 1921	14.7	4.2	24.3	1.8	0.7	2.7	6384	2341
	1922	80.2	18.5	50.9	5.8	2.2	3.8	10777	3085
c	ML, tops, 1921	5.3	4.8	12.4	2.3	0.4	2.1	2883	1199
	1922	22.4	25.2	7.9	3.1	2.8	8.1	3508	2232
	ML, valleys, 1921	8.2	3.7	14.4	1.7	0.6	2.2	1432	1432
	1922	60.9	17.1	16.7	4.0	3.6	4.3	5140	2205
<i>Mean values:</i>									
d	All tops, 1921	8.2	4.3	16.5	1.8	0.70	2.31	4100	1174
	1922	25.9	14.9	15.0	2.8	2.60	6.80	3755	2270
	Valleys, 1921	29.8	5.3	21.7	3.8	1.76	1.83	4350	1790
	1922	56.4	16.5	26.2	3.8	4.43	4.88	6470	2390
e	Increase shown by tops:	216 %	247 %	-9.0 %	55 %	271 %	194 %	-8.3 %	+93 %
	Increase shown by valleys:	89 %	212 %	21 %	0.0 %	152 %	167 %	49 %	34 %
	General increase on basis of all samples taken:	151 %	199 %	3.5 %	48 %	195 %	190 %	2.5 %	77 %

Table VII. *Sections d' and e'.*

(The Table gives the mean values for the water contents and coefficients of humidity for high and low ground in dry and wet seasons calculated as in Table VII, sections d and e, but ignoring the 4 line which is anomalous through having been in part recently burnt.)

	Position of samples and year	Water content		Coefficient of humidity		Humus	
		2"	9"	2"	9"	2"	9"
d'	All tops, 1921	9.7	5.2	0.77	2.29	15.8	2.2
	1922	27.9	17.9	2.65	6.86	15.8	3.5
	Valleys, 1921	12.0	4.0	0.69	2.20	19.4	1.75
	1922	73.1	17.8	5.72	3.96	33.6	4.9
e'	Increase shown by tops	188 %	244 %	242 %	200 %	0.0 %	59 %
	Increase shown by valleys	510 %	345 %	758 %	80 %	73 %	180 %
e'	General increase on basis of all samples taken except the 4 line:	247 %	265 %	325 %	179 %	14 %	81 %

Concerning the effects of a wet season on the redistribution of soluble salts it would appear from a superficial glance at the figures in the last columns of Table VII d that the effect has been to cause a considerable increase in the conductivity of the 9-inch depths (93 per cent.) on the tops at the expense of the 2-inch depths and an all round increase in the valleys. The appearance happens to be roughly correct in so far as the valleys are concerned but is misleading for the tops, since in taking the changes in the amounts of soluble salts as an indication of the leaching effects it is evidently not sufficient to take only the actual salt concentrations into account but the salt concentrations compared with the percentage of humus. If the amount of humus present be also taken into account it is found that there is a general loss by both depths at the tops and a general gain by both depths in the valleys, the 2-inch depths in both cases changing by the greater amount. Thus the lower layers (9-inch) on the tops do not gain in salts by leaching from the upper layers as appears from Table VII d, but the apparently greater quantities of soluble salts in the 9-inch depths are only due not to leaching but to an incidental increase in the percentage of humus. The true effects of leaching during the wet season may be gathered from Table VII f in which the ratios of total salts/humus are compared for the different layers in the two seasons. The changes in this ratio are taken to be a fairer indication of the leaching or drainage effects than those in actual conductivity, since changes in the latter are not only due to leaching but also to variations in the amount of humus present.

It is taken, moreover, that a measure of the effect of leaching or drainage on any part of a slope is given by the difference between the change in salts/humus ratio for the relevant part of the slope and the aggregate change for the whole slope. Thus supposing that there were found to be in one year an aggregate increase in the amount of salts per unit amount of humus of 1 per cent. it is taken that if no leaching or drainage occurred the salts/humus ratio at all points on the slope would show an approximately uniform increase of 1 per cent. If now leaching or drainage cause a redistribution of the salts the ratio will decrease in some places and increase in others. If in some particular region the ratio were found to have increased by 5 per cent. the drainage or leaching effect would be taken to be proportional to 4, since there would have been an increase of 1 per cent. without any leaching and the leaching has accounted for an additional change of 4 per cent. If in another part there were no change in the ratio leaching would have accounted for a loss of the 1 per cent. that would have been normally gained if no leaching had occurred. The leaching effect on any soil given in Table VII f therefore is the difference between the percentage change in the ratio of salts/humus for the relevant part of the slope and the aggregate percentage change in the ratio for the whole slope.

Table VII f. *Changes in the salts/humus ratio and the effect of leaching and drainage from 1921 to 1922.*

Soil samples from which the results are calculated	Year	Mean values of ratio of total salts/humus	
		2"	9"
Means based on all samples taken from the 4-, 12- and middle lines (35 samples in 1921 and 40 in 1922 from each depth)	1921	308	690
	1922	427	648
Increase	—	38 %	— 6 %
All tops	1921	326	730
	1922	439	674
Increase	—	34.5 %	— 7.7 %
Leaching effect	—	3.5 % loss	— 1.7 % loss
All valleys	1921	224	511
	1922	372	536
Increase	—	66 %	— 5 %
Leaching effect	—	27.2 % gain	— 11 % gain

It will be seen from the table (VII f) that the leaching effect on 2-inch depths on high ground has been to cause a loss of 3.5 per cent. since there has only been a gain of 34.5 per cent. instead of 38 per cent., and the effect on 9-inch depths on high ground has been to cause a loss of 1.7 per cent. as the decrease is 7.7 per cent. instead of only 6 per cent. and so on. The means¹ at the beginning of the table show that there has been a general increase in total salts during the year's interval of 38 per cent. in the 2-inch depths and a slight decrease (6 per cent.) in the 9-inch. In the aggregate then there is no gain in salts by loss through leaching from the upper layers. If leaching due to greater rainfall played a part in increasing the salts at 9-inch depths at the expense of the supply in the 2-inch depths a greater increase in the concentration of salts per given amount of humus should be found in the 9-inch layers after a wet season than in the 2-inch layers but actually on the tops the proportion of salts to humus in the 9-inch layers has decreased and in the valleys has only increased to less than half the extent shown by the 2-inch depths. It is to be concluded that there is a general loss on the tops, the 9-inch layers losing more by drainage than they receive by leaching, and a large increase in the valleys which is much more pronounced in the 2-inch depths than in the 9-inch.

Table VII g. *Ratios of $\frac{\text{salts/humus for wet season}}{\text{salts/humus for dry season}}$.*

Mean values:			
2" tops	1.345	All tops	1.05
9" tops	0.923	All valleys	1.24
2" valleys	1.660	All 2" depths	1.61
9" valleys	1.050	All 9" depths	0.974

¹ Founded on 37 samples in each year from each depth.

Table VII h. *Salts/humus ratio for the 12 line slope in 1921 and 1922.*

		Salts 2"	Humus 2"	Salts/humus ratio 2"
Top, 12 AB	{ 1921	6250	32.7	191
	{ 1922	6666	36.4	183
Bottom, 12 12 Z	{ 1921	6890	29.4	234
	{ 1922	18150	92.8	195

That the wet season does not cause the 9-inch layers to gain appreciably at the expense of the 2-inch is also seen from the figures in Table VII g which not only bring out the greater increase on the low-lying ground at the expense of the high in a wet season but also show that the salts/humus ratio has increased in the aggregate to 1.61 times its original value in all the 2-inch depths taken together and has decreased slightly, to .97 of its original value, in the aggregate 9-inch depths.

The effects of leaching on burnt ground will be dealt with below.

THE EFFECTS OF FIRES.

The effects of fires on the soil are shown in Table VIII, the first part of the table giving the results in individual cases as shown by comparing the properties immediately before and immediately after the fires and the last part of the table giving the aggregate results as shown by means.

It will be noticed (cf. Fritsch and Salisbury (10)) that on the average a fire leads to the destruction of 60 per cent. of the original humus in the surface soil (leaving, e.g., 8.6 per cent. instead of 20.9 per cent.) and only about 8 per cent. of that lower down at the 9-inch level. The effects, however, are distinctly different according to the age and height of the vegetation that is burnt and the consequent actual total amount of humus originally present in the soil. In relatively young heaths, burning, it will be seen, leads to the destruction of 66 per cent. of the original organic matter in the 2-inch depths, but in the case of very old heath, bearing *Calluna* to a height of 3-4 feet and with a very high original percentage of humus, as much as 70 per cent. of the original humus may remain after firing. In consequence of the destruction of the humus the water content of the 2-inch layers falls on the average to about one-third of its original value, but that of the deeper layers is practically unaffected or may slightly increase through the more ready percolation (see page 59) from the upper layers.

Concerning the effects on the concentrations of soluble salts, it is to be supposed (see below) that the immediate effect is always to increase the total salts though this can only be demonstrated in soils where a large amount of humus is left after burning and the analysis can be made at a very short interval after the fire. It is only shown in Table VIII in the case of 12 AB, the only one where these conditions were obtained, but is probably a general feature and due to the liberation of salts from the burnt plant remains.

A few months after the fire, as shown by the means at the bottom of the table, the general effect is a decrease in total salts both in the 2-inch and 9-inch depths. The resulting reduced concentration of salts is on the aggregate about 70 per cent. of the original concentration in 2-inch depths and 86 per cent. of the original in 9-inch depths. The results are explained by the more ready leaching after the destruction of the humus (see p. 59) and naturally the effect is, as shown by the table, greater in the surface than in the lower layers. Burning then leads to a serious loss of salts, since the leaching effects when the humus is destroyed more than balance the gains of salts from the plant remains.

Table VIII. *Effect of burning.*

	Soil sample	Burnt in		Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
				2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
Young heaths	4 A	1923	before	30.3	10.6	11.9	2.2	3920	1350	2.54	4.81	328	613	3.2	3.9
	"	"	after	9.6	7.8	8.5	2.3	2700	1105	1.13	3.39	318	480	3.3	3.2
	4 AB	1923	before	13.5	6.8	5.6	0.6	2320	793	2.41	11.42	415	1320	3.1	3.6
	"	"	after	8.2	—	4.9	—	1598	—	1.67	—	326	—	3.4	—
	4 BC	1923	before	7.2	5.6	36.8	2.2	3030	1340	0.20	2.55	82	609	3.4	4.0
	"	"	after	6.2	—	1.3	—	914	—	4.70	—	704	—	3.5	—
	15 D	1924	before	—	—	7.6	—	1520	—	—	—	200	—	3.6	—
	"	"	after	—	—	6.0	1.5	1197	624	—	—	199	416	3.8	4.1
	4 A-C	1923	before	17.0	7.7	18.1	1.7	3090	1161	1.38	6.26	275	847	3.2	3.8
	aver.		after	8.0	7.8	4.9	2.3	1737	1105	2.50	3.39	449	480	3.4	3.2
Old heaths	12 AB	1924	before	41.7	1.7	36.4	13.3	6666	602	1.15	0.13	184	45	3.3	4.0
	"	"	after	—	—	—	—	7140	—	—	—	—	—	3.3	—
	12 A	1924	before	31.5	—	27.3	—	5780	—	1.15	—	212	—	2.7	—
	12 B	"	after	—	—	22.4	—	2435	—	—	—	109	—	3.5	—
Mean values for			before	36.6	1.7	31.8	13.3	6223	602	1.15	0.13	198	45	3.0	4.0
oldest heath			after	—	—	22.4	—	4787	—	—	—	109	—	3.4	—
Means for younger heath			before	17.0	7.7	15.5	1.7	2698	1161	1.72	6.26	256	848	3.3	3.8
			after	8.0	7.8	5.2	1.9	1602	864	2.50	3.39	387	448	3.5	3.6
Means of all values together			before	24.8	6.18	20.93	2.07	3872	1021	1.49	4.73	232	647	3.2	3.88
			after	8.0	7.80	8.58	1.90	2664	864	2.50	3.39	331	448	3.5	3.65

Repeated burning would therefore lead to a steady impoverishment of the heath in this respect and since as will be seen from what follows it would also lead to a steady decrease in acidity it might be expected to cause a degradation of the heath. Such has already been observed to be the case by Fritsch and Salisbury (10), so that the above results merely go to explain the facts already established.

The acidity of the surface layers after burning is invariably found to decrease, the mean results showing a change in pH from 3.2 to 3.5 (Table VIII). On the other hand the acidity of the deeper layers is found to increase slightly owing apparently to their more readily receiving the more acid leachings from the upper layers, as a result of which they become almost as acid as the surface soil. Burning thus leads to a general decrease in acidity, partly no doubt caused by the liberation of plant bases and partly by the destruction of organic acids. Since it is also evident that fires lead

to the destruction of much of the colloidal matter of the soil (see below), it is of interest to recall in this connection that McCool and Wheeting (21) found that artificial removal of the colloids from soil by Chamberland filtration led to a decrease in H^+ concentration and a decrease in the amount of lime water necessary for neutralisation. The effect is probably due to the elimination of apparent acidity due to the selective adsorption of bases by the colloids, so the partial elimination of this effect by the destruction of colloids may possibly play a part in the lowering of acidity when the colloids are destroyed by fires. Burning also tends to equalise the acidity at different layers, a tendency which runs side by side with that towards equalisation of texture.

The coefficient of humidity appears to decrease somewhat both in the surface and 9-inch layers, but this is not shown in the 2-inch layers in the means owing to one anomalous result (4 BC). Neglecting this result it will be seen (Table VIII) that the salts/humus ratio as would be expected is increased considerably in the surface layers as a first effect though this condition is not maintained but regularly falls off with time (see Table X), while in the 9-inch layers the ratio decreases, probably owing to the increased exposure to washing out by rain. It is evidently this same factor which accounts for the salts/humus ratio falling off again in the 2-inch layers, though here it naturally takes longer to produce an effect than in the 9-inch layers owing to the greater amount of remaining humus. The retentive power of the surface layers is, however, so impaired as a rule by firing that they may show a continued loss of salts by leaching for as much as three or four years after the fire, and it is only after this time has elapsed and the soil is almost completely covered again by vegetation that the amounts of soluble salts again begin to increase, through the rate of production again coming to exceed that of loss. This is well shown in the case of the soils from 12 I and 2-3 Y in Table X, where there is seen to be a regular falling off of the augmented ratio value during successive years after the fire. This is undoubtedly due to the destruction of the soil colloids which are naturally not appreciably replenished until a fairly late stage in recolonisation. The destruction of the colloidal matter is clearly evidenced by the difference between the percentages of water retained in air by burnt and unburnt soils. The averages of 65 and 57 analyses respectively show that the mean values of this "hygroscopic moisture" for unburnt soil are 4.3 per cent. for the 2-inch layers and 1.3 per cent. for the 9-inch depths, whereas after burning the 2-inch layers only retain 0.65 per cent. and the 9-inch 0.9 per cent. Naturally again the greater difference is in the 2-inch layers since it is unlikely that any very marked direct effect of firing would be felt at the 9-inch depths.

Table IX. *Recovery from burning.*

Soil	Year of fire	Year of analysis	Water content		Humus		Total salts		pH		Salts/humus ratio		Interval after fire in years
			2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	
12 I	1922	1922	13.8	10.5	3.5	1.2	1800	1075	3.8	4.6	515	895	$\frac{1}{2}$
4 XY	1920	1921	1.2	4.4	17.3	1.2	4540	1099	—	—	265	919	1
4 YZ	1920	1921	3.0	3.2	10.3	1.6	2380	552	—	—	231	345	1
4 4Z	1920	1921	70.6	8.1	50.5	6.4	7410	2667	—	—	147	417	1
12 I	1922	1923	10.2	7.9	4.2	1.2	1535	1019	2.9	3.7	365	814	$1\frac{1}{2}$
ML 0-9	1919	1921	7.6	7.0	17.6	3.9	3945	1179	—	—	233	328	2
4 XY	1920	1922	12.9	8.5	6.7	2.2	2320	1430	3.6	3.8	346	650	2
4 YZ	1920	1922	15.4	7.8	5.6	1.8	2500	1148	3.4	3.8	446	637	2
4 4Z	1920	1922	59.5	17.7	31.8	2.3	7400	2468	3.2	3.5	233	1073	2
2-3 Y	1920	1922	25.9	—	10.8	11.5	3840	1390	3.5	—	356	121	2
4-5 WX	1920	1922	25.8	6.0	10.2	2.4	6240	1850	3.2	3.9	611	770	2
3-4 YZ	1920	1922	4.1	7.5	3.2	0.6	1550	819	3.8	4.5	484	1366	2
ML 0-9	1919	1922	24.1	18.3	8.3	4.4	3577	2668	3.5	4.0	466	602	3
2-3 Y	1920	1923	8.3	—	9.3	—	2740	—	2.5	—	295	—	3
4-5 WX	1920	1923	—	—	0.6	—	2790	2125	3.6	3.2	4650	—	3
3-4 YZ	1920	1923	4.6	3.8	3.5	2.0	1678	950	2.9	3.0	480	475	3
2-3 Y	1920	1924	—	—	8.1	—	1560	—	4.0	—	193	—	4
3-4 YZ	1920	1924	—	—	—	2.0	—	615	—	4.0	—	307	4
36 B	1913	1921	15.4	—	41.8	—	6670	—	—	—	160	—	8
38 B	1913	1921	7.9	—	14.7	—	2598	—	—	—	177	—	8
40 B	1913	1921	12.9	—	21.2	—	4250	—	—	—	201	—	8
27 C	1912	1921	17.2	—	18.8	—	5880	—	—	—	313	—	9
28 C	1912	1921	9.4	—	18.7	—	3167	—	—	—	170	—	9
30 C	1912	1921	4.0	—	11.8	—	2172	—	—	—	184	—	9
36 B	1913	1922	21.8	—	9.4	—	3120	—	3.3	—	322	—	9
38 B	1913	1922	—	—	7.2	—	2560	—	3.6	—	356	—	9
40 B	1913	1922	—	—	11.6	—	6650	—	3.0	—	574	—	9
27 C	1912	1922	13.5	—	4.5	—	2525	—	4.1	—	561	—	10
28 C	1912	1922	21.9	—	10.6	—	2700	—	4.0	—	255	—	10
30 C	1912	1922	16.7	—	5.0	—	2170	—	3.8	—	434	—	10
36 B	1913	1923	8.6	—	12.2	—	3508	—	3.1	—	288	—	10
38 B	1913	1923	7.6	—	10.9	—	3770	—	3.1	—	349	—	10
40 B	1913	1923	34.7	—	15.6	—	5120	—	2.9	—	328	—	10
27 C	1912	1923	9.2	—	14.8	—	4255	—	2.5	—	288	—	11
28 C	1912	1923	3.5	—	5.7	—	1910	—	3.3	—	335	—	11
30 C	1912	1923	8.1	—	7.0	—	2220	—	3.0	—	317	—	11

Table X. *Leaching after burning.*

Soil	No. of years after fire	Salts/humus ratio	
		2"	9"
12 I	$\frac{1}{2}$	515	895
12 I	$1\frac{1}{2}$	365	815
2-2 Y	2	365	—
2-2 Y	3	295	—
2-2 Y	4	195	—

Table XI. *Recovery from burning.*

The table gives mean values for groups of soils from Table IX which are of the same age after burning.

Age of soil or interval after fire in years	Water content		Humus		Total salts		Salts/humus		pH	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
$\frac{1}{2}$	13.8	10.5	3.5	1.2	1800	1075	515	895	3.8	4.6
1	24.7	5.2	26.0	3.1	4777	1437	214	559	—	—
$1\frac{1}{2}$	10.2	7.9	4.2	1.25	1535	1019	365	814	2.9	8.7
2	21.6	8.1	12.3	3.5	3971	1470	387	707	3.5	3.8
3	12.3	11.1	5.4	3.2	2696	1914	1473	538	3.1	3.4

Table XII. *Leaching on slopes after burning.*

		Salts/humus ratio						
Years after fire ...		1		2		9	10	11
Soil		2"	9"	2"	9"	2"	2"	2"
Tops	{ 4 XY	262	914	346	650	—	—	—
	{ 36 B	—	—	—	—	332	228	—
	{ 27 C	—	—	—	—	—	516	287
Middles	{ 4 YZ	231	345	445	638	—	—	—
	{ 38 B	—	—	—	—	365	349	—
	{ 28 C	—	—	—	—	—	354	334
Bottoms	{ 44 Z	147	416	233	1072	—	—	—
	{ 40 B	—	—	—	—	573	328	—
	{ 30 C	—	—	—	—	—	434	319

Table XII a.

Giving average values for the salts/humus ratio for high and low ground in two successive years of observation, calculated from the figures in Table XII, above.

		Salts/humus		Increase %		Leaching effect*	
		2"	9"	2"	9"	2"	9"
Means of all observations, 1st year		356	558	—	—	—	—
2nd year		325	787	-8.7	71.0	—	—
Tops,	1st year of observation	370	914	—	—	—	—
	2nd " "	307	650	-17.1	-28.8	-8.4	-100
Middles,	1st year	313	345	—	—	—	—
	2nd " "	376	638	20.0	85.0	28.7	13.6
Bottoms,	1st year	385	416	—	—	—	—
	2nd " "	293	1072	-24.0	158.0	-15.3	86.6

* = difference between actual increase and the mean increase shown in the first line of the table.

The general effects of leaching on burnt areas are roughly similar to those already described for unburnt areas as far as the surface layers are concerned, namely a loss of salts at the top of the slope and a gain at the base (cf. p. 49), as shown in Tables XII and XII a. Unlike the unburnt slopes, however (cf. Table VII f), the effect instead of being less at the 9-inch depths is far more marked than in the 2-inch depths, the 9-inch layers at the tops of the slopes losing in the aggregate 28 per cent. of their salts instead of gaining 71 per cent., so that the leaching effect is proportional to 100, and the 9-inch layers at the base acquiring double their original salt content. On more or less recently burnt slopes, as will be seen from the table (XII a), the 9-inch layers in the middles and at the bottoms of the slopes do increase in their salt content through leaching from the surface and 9-inch soils at the tops. All the normal effects are therefore as would be expected much more pronounced on the burnt than on the unburnt slopes, but the retentive properties of the surface soils are so impaired that even the lowest 2-inch soils here, unlike those on unburnt slopes, appear to lose more by leaching than they receive by drainage.

The means at the top of the table (XII a) show distinctly the gain here by the 9-inch layers at the expense of the 2-inch, but the gains by both

depths in the middles of the slopes appear to be almost without explanation. For some reason it appears that the middles were by far the poorest regions in salts before the fires so that on the increased supplies of drainage water they could themselves gain salts from above but at the same time pass on a solution sufficiently weak to cause further washing out of salts from the 2-inch depths lower down the slopes. A clue to the mechanism of this gain by the middles and simultaneous loss by the valleys immediately below may lie in the fact that the middles only receive drainings from one direction, and these may be very concentrated through the ready leaching from burnt ground above, whereas the valleys will be washed by larger quantities of drainage water from possibly three different directions, and this water, coming, as it may, in large part from ground that has not been recently burnt, is likely to be much more dilute than the solution received by the middles of the slopes.

To summarise then the effects of burning on salt content it may be said that the first effect is to increase the total salts present (see 12 AB in Table VIII and the abnormally high values at the beginnings of Tables X and XI). The added salts are then rapidly diminished by leaching (Table X) and the reduction continues until colonisation and the production of new humus check the process and cause the salts/humus ratio again to increase (Table XI). The decrease through leaching is much more pronounced than on unburnt ground, especially in the 2-inch depths in the valleys, and goes on for longer on the upper parts of the slopes than on the lower, the lower ground soon regaining salts through leaching from above. The lower ground would then perhaps be expected to be more hospitable for colonisation than the upper and as compared with older land would be more favourable for the development of deeper rooting forms such as *Calluna* and *Ulex nanus* (cf. Fritsch and Salisbury (10)) through the relatively higher salt content of its 9-inch layers.

RECOVERY FROM BURNING.

The process of recovery from burning is best illustrated by Table XI which gives the mean results calculated from the data in Table IX. In this table (XI) averages have been taken for all soils of the same age since the last fire (i.e. with which equal intervals have elapsed since last being burnt). It shows a gradual increase in acidity during the first three years from a pH of 3.8 to 3.1 in the 2-inch layers and from 4.6 to 3.4 in the 9-inch layers and also serves to illustrate the march of changes in the salts/humus ratio. After the first few months the ratio is still high but falls to a minimum about the end of the first year, after which it again regularly increases. This is well seen in the 2-inch depths but is not so distinct in the 9-inch, as the last two values appear too low. The increase in the actual quantity of humus is best realised by comparing the percentages shown in the 1922 and 1923 analyses

of soils from 36 B, 38 B, 40 B, 27 C, 30 C, 12 I and 3-4 YZ (see Table IX). As would be expected the increase is a general phenomenon in recovering soil, the relatively few examples which may be found in the tables where the reverse appears to take place (e.g. 28 C and 4-5 WX) being fully explained by incidental causes such as reburning, but some of these cases will be discussed later.

EFFECT OF HEIGHT ON SLOPES.

Results have been collected in Table XIII to show the variations in water content, humus content, total salts and acidity at different heights on slopes. In each group of figures the top line gives the value for tops, the next the intermediate value or values at half way heights and the bottom one the figures for the valleys. It will be observed that the water content is almost invariably considerably greater at the bottoms of the slopes than on the tops but that general rules cannot equally well be laid down for humus content, acidity or content of total salts. With respect to humus the figures are not at all diagrammatic but show few exceptions to the general rule that there is usually distinctly more humus in the valleys. That this is the general rule is clearly brought out by the means shown at the end of the table (XIII), which it will be seen bear a fairly good relation to the individual cases, and also by a comparison of the humus contents for tops and valleys already given in Table VII d. In Table XIII also the aberrant figures are readily explained by the differences in the character of the vegetation at the different heights which are brought about by the erratic nature of some of the past fires. Other things being equal, i.e. with the same association at the same stage throughout the whole slope, there is more humus in the valleys as brought out by the groups of figures in Table XIII, the bottom figures in these groups being usually greater than the top ones.

The total salts are usually greater in the valleys than on the tops, this point being shown both by Table XIII and Table VII. The reason appears to be twofold: firstly, the higher water content (see Table VII) favours a more luxuriant growth and a greater formation of humus and secondly, the low ground, as established in Table VII f, receives leachings from the higher.

In the case of acidities the gradient may be either upwards or downwards, i.e. the upper part may be more acid than the lower or *vice versâ*. Acidities on slopes cannot therefore be said to run side by side with water content or humus, but the determining factor appears to be the nature of the valley vegetation, which is more variable than that of the summits. It will be seen from the table (XIII) that the mean results show a greater acidity in the valleys and that this also holds in six out of the nine individual cases. It has been shown by Conner ((5) and (6)) that soils rich in organic matter showed greater acidity when fully saturated and those low in organic matter were more acid when only half saturated, so that if differences in the water and humus contents were responsible, it appears that the opposite relation

Table XIII. *Variation of properties with height of slope.*

Slope	Age of vegetation in years	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH		
		2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	
F 1	9	36 B	21.8	—	9.4	—	3120	—	2.5	—	332	—	3.3	—
		38 B	—	—	7.2	—	2560	—	—	—	355	—	3.6	—
		40 B	—	—	11.6	—	6650	—	—	—	573	—	3.0	—
F 2	10	27 B	13.5	—	4.5	—	2325	—	3.0	—	516	—	4.1	—
		28 B	21.9	—	10.6	—	2700	—	2.1	—	255	—	4.0	—
		30 B	16.7	—	5.0	—	2170	—	3.3	—	435	—	3.8	—
Valley A, west, 4 line	2	12.9	8.5	6.7	2.2	2320	1430	1.9	3.9	346	650	3.6	3.8	
		15.4	7.8	5.6	1.8	2500	1148	2.8	4.3	446	638	3.4	3.8	
		59.5	17.7	31.8	2.3	7400	2468	1.9	7.7	232	1072	3.2	3.5	
Valley B, west, 4 line	6	10.8	7.0	4.5	0.5	2350	627	2.4	13.8	522	1254	3.0	4.3	
		18.6	13.4	1.7	3.0	2895	2220	1.1	4.4	1700	740	3.5	3.8	
		13.4	15.2	14.9	2.6	2172	2172	0.9	5.9	146	835	3.9	4.2	
<i>Erica</i> slope	8	12.5	16.2	4.6	2.8	2102	2322	2.7	5.8	456	828	3.9	4.0	
		21.9	—	16.0	1.25	5700	1098	1.4	—	356	878	3.1	3.4	
		11.2	5.9	5.1	2.45	2560	1050	2.2	2.4	505	428	3.2	3.8	
Opposite <i>Erica</i> slope	7	27.0	9.3	25.2	3.14	5000	1885	1.1	3.0	199	600	3.3	3.3	
		39.7	8.5	28.3	3.7	6250	1910	1.4	2.3	221	515	3.3	3.7	
		34.8	34.3	16.3	1.9	4540	1665	2.1	18.0	278	875	3.5	4.0	
		14.8	5.7	2.2	0.6	1784	533	6.6	9.5	810	888	3.4	4.0	
		—	8.2	—	6.1	—	1430	—	1.3	—	234	—	3.7	—
		29.5	102.5	10.1	2.4	3635	1480	2.9	42.7	360	615	3.4	3.3	
Valley A, east, on the 4 line	6	92.1	25.6	5.07	4.3	4030	2500	1.8	6.0	795	581	3.8	4.1	
		20.7	—	8.9	2.9	3920	1072	2.3	—	440	370	3.2	3.6	
		16.6	6.8	36.8	2.2	3032	1340	0.5	3.1	82	610	3.4	4.0	
		13.5	6.8	5.6	0.6	2320	793	2.4	13.0	414	1320	3.1	3.6	
		30.25	10.6	11.9	2.2	3920	1350	2.5	4.8	330	613	3.2	3.9	
		59.5	17.7	31.8	2.3	7400	2468	1.9	7.7	232	107	3.2	3.5	
Valley B, west, on the 12 line	Over 15	7.1	21.8	2.6	7.7	1885	3030	2.7	2.8	725	394	3.9	3.2	
		10.1	7.6	2.3	—	1428	722	4.4	—	620	—	3.8	4.3	
		18.5	9.5	7.1	3.4	2752	1738	2.6	2.8	387	510	3.5	3.5	
Valley A, east, on the 12 line	Over 15	41.7	9.5	17.8	2.3	6450	2630	2.3	4.1	363	1144	2.9	3.8	
		64.7	8.3	21.9	1.04	5710	1000	3.0	8.0	251	960	3.2	4.2	
		41.7	—	36.4	—	6666	—	1.1	—	183	—	3.3	—	
Means:	All tops	89.4	26.6	97.9	9.6	10000	4760	0.9	2.8	102	496	2.9	3.1	
		133.5	20.7	92.8	8.4	18150	425	1.4	2.5	195	506	2.9	4.1	
		23.1	16.1	10.1	2.5	3451	1417	2.3	7.1	418	767	3.4	3.8	
	Intermediates	24.8	18.6	17.5	3.1	3430	1615	2.3	8.8	481	656	3.4	3.64	
		56.9	16.6	25.4	3.7	6820	2103	2.1	5.2	390	679	3.3	3.8	

should hold and that the greater acidity should be found on young heaths at the tops and on old heaths in the valleys, where there is a higher water content. Thus in old ground acidity and water content should run parallel, if the rule applies, and the greater acidity be found in the valleys, while shortly after fires the reverse should be true, but such is not the case (see especially Valley A, west, 4 line in Table XIII). The effect is therefore apparently not merely related to the water content or humus, but depends as suggested above upon the nature of the vegetation at the bottom of the slope. It is significant that in the three cases where the valley was found to be less acid, the base of the slope was occupied by a special zone of *Ulex europaeus* and *Pteris*. A particularly well marked zone of this type existed also at the junction of the valleys A and B round 20-21 YZ and special samples from this region showed that such zones were associated

with a lower acidity, the *pH* being only 3.9. This appears to be the explanation of the lower acidities at the bases of the three slopes in question, viz. valley B, west, 4 line, the *Erica* slope and opposite the *Erica* slope. The last named is particularly suggestive, as the type of vegetation here only changed at the very base and it is accordingly only the last *pH* value going downwards which shows the decreased acidity, the intermediates showing the normal tendency to rise towards the valley.

In the six cases which obey the rule of higher acidity in the valley it is further to be observed that the effect is very much more pronounced in the case of the oldest vegetation such as that of the 12 line slopes at the bottom of the table than in the younger slopes. This may be related not only to the direct effect of the greater percentages of humus on these slopes, especially at the bases, but also to the fact that less drainage appears to take place on the old ground than on the young, so that the valley acidity would be less ameliorated by washing through with drainage water than it appears to be on the younger slopes. The drainage effect and washing out of the valleys evidently decrease markedly with increasing age of the vegetation. Owing to the accumulation of large quantities of humus water is retained instead of being allowed to wash out the lower layers and is re-evaporated from positions high on the slopes. This theory that there is less travel of drainage water down the slopes on old ground is supported by the figures given in Table VII h for the changes in the salts/humus ratio at the top and bottom of the 12 line slope between 1921 and 1922, which testify to the lack of drainage effects here as compared with other slopes. It will be remembered that in the aggregate (Table VII f) the salts/humus ratio increased for 2-inch depths by 38 per cent. in the year, but after the wet season had increased in the valleys more than on the tops owing to the washing of salts down the slopes. Here, however, there is no general increase (Table VII h), probably because the zone was already so old as to have reached a state of equilibrium. It therefore only shows a loss of salts from the 2-inch layers to its 9-inch depths, and in the valley the salts/humus ratio has actually fallen off rather more than on the top, showing the lack of drainage effects down the slope. Possibly the gradual elimination of this drainage effect with vegetation of increasing age may be a factor favouring the development of a much higher acidity in the valleys as compared with the tops.

EXPERIMENTS ON THE PERCOLATION OF WATER AND SALT SOLUTIONS THROUGH BURNT AND UNBURNT SOILS.

It has been assumed in a number of connections in the foregoing sections that a soil after burning would more readily allow water and salts to drain through it than an unburnt soil, and that in consequence salts would be more readily leached on burnt areas and would be more readily drained to the lower levels of a burnt slope than an unburnt.

It seemed advisable therefore to make a few laboratory experiments upon burnt and unburnt soils to establish that this is actually the case. Experiments have therefore been carried out on the permeabilities of different samples of water and salts, the permeability of the unburnt soil being found first and then compared with that either of a natural burnt soil or a soil artificially slowly heated until the organic remains appeared to be charred to approximately the same extent as is found in the field shortly after a fire.

The Percolation Rates with Water.

The permeability to water was roughly determined by finding the time required for the water level in a long glass tube of 3 cm. diameter and containing a column of soil 20 cm. high supported on gauze at its lower end to rise 10 cm. under a pressure of 20 inches of water. The soil was in all cases very carefully packed into the tube and as uniformly as possible, the final pressure used being always that which would just cause the column to slide in the tube. The upper limit of the column was defined by a piece of gauze supported by a glass rod so as to keep the packing uniform and the column the same length. The method is admittedly very rough but seemed sufficient for the present purpose and the values as given below are sufficiently different to be significant. The times taken were as follows:

Unburnt soil		Collected burnt soil		Artificially burnt soil	
5 mins.	5 secs.	1 mins.	46 secs.	0 min.	43 secs.
3	43	2	0	—	—
4	37	1	26	1	0
4	30	—	—	—	—
8	10	2	0	0	43
11	40	0	44	—	—
11	50	0	50	1	0
Means: 7 mins. 4 secs.		1 min. 20 secs.		0 min. 54 secs.	

It is then evidently quite legitimate to assume that drainage is much facilitated by burning whether in the laboratory or in the field.

Rates of Drainage of Salts.

The leaching and drainage rates of burnt and unburnt soils collected from about 2-3 X were compared by the following method. A column of soil 20 cm. high, carefully and uniformly packed as in the determination of percolation rates (see above), was supported by a piece of wire gauze resting on the inturned edge of a glass tube 3 cm. in diameter and 50 cm. long, the soil having been air-dried and crumbled before packing. The tube was marked at 10 cm. above the soil level (the volume of the tube between the top of the soil and the mark being roughly 66 c.c.). The soil was then thoroughly washed through from above with tap water at a constant head of 10 cm. for half an hour until the water draining through had a constant conductivity. The resistance of the drainings was measured at intervals and it was found,

as would be expected, that their concentration was greatest at first and fell off with time but that with unburnt soil it eventually fell to about half the concentration of the tap water which was being supplied at the top. The soil therefore gives up electrolytes to the washings at a decreasing rate but in the end must be absorbing electrolytes from the in-going solution. The reason for this behaviour is not altogether clear, but it suggests either that the tap water happens to contain electrolytes which are more readily absorbed by the soil than are the substances which were originally present, or that some substance in the tap water forms a compound with something present in the soil which is either insoluble or less dissociated.

When the drainings reached a constant conductivity the liquid over the soil was allowed to drain just to the soil level and replaced by 50 c.c. of 1 per cent. Tidman's sea salt solution with which the tube was kept filled to the mark by means of a dropping funnel supported above. The emerging solution was allowed to fall into 1000 c.c. of distilled water in a reservoir below and the rate of increase of conductivity of this water was measured by successive readings for half an hour, the rate of increase being taken to give a measure of the facility of salt-drainage through the soil.

After half-an-hour the salt solution was allowed to drain to the soil level and the tube was again kept filled to the mark with tap water. The conductivities of successive five minute fractions of "leachings" were then measured to find the rate or the facility with which the salts could be washed out. The results are set out in Table XIV and plotted in Fig. 3.

The results indicate that although the burnt soil showed more absorption at the very beginning, its leachings coming out initially less concentrated than those from the unburnt soil, it allowed its leachings continuously to increase in concentration for 15 minutes and then only retained sufficient salts from the tap water to reduce the concentration of the latter by 15 per cent., whereas the unburnt soil allowed no increase in the concentration of its leachings from the beginning, absorbed electrolytes from the tap water continuously from the fifth to the 107th minute after the start and reduced its concentration to 53 per cent. It might be argued that the conductivity of the leachings from the burnt soil is still high at the end of half-an-hour because it has only been giving up its salts slowly, and that that from the unburnt soil is already low because it has lost all its salts quickly and has no more to lose. If, however, this were the correct interpretation, obviously the values of the resistance of the solution from the burnt soil should have been *rising* to their final value and those of the unburnt soil should have been falling. The reverse is true in both cases so evidently the first interpretation is the correct one and the unburnt soil is the more retentive of absorbed salts.

In the second part of the experiment it is seen that in equal times the burnt soil allowed $2\frac{1}{2}$ times as much water to pass as the unburnt soil and

*Amount of Salts Lost.
(Conductivity of water in reservoir.)*

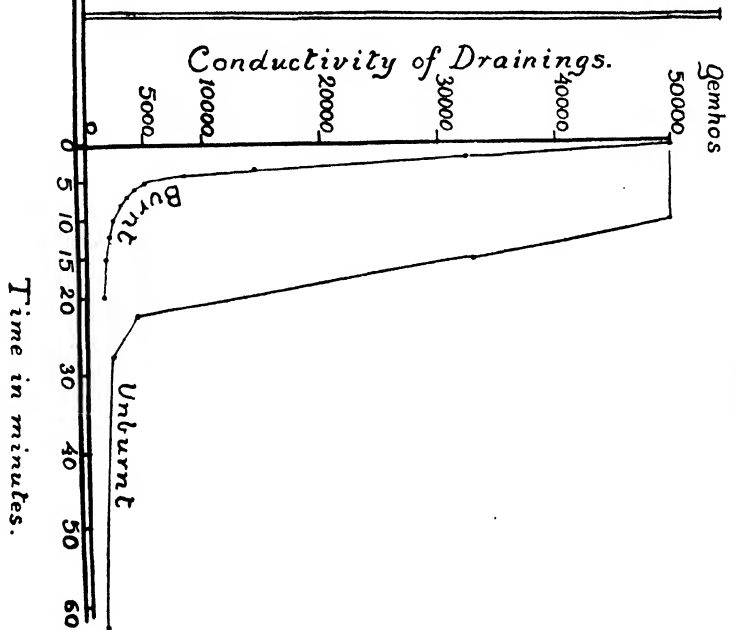
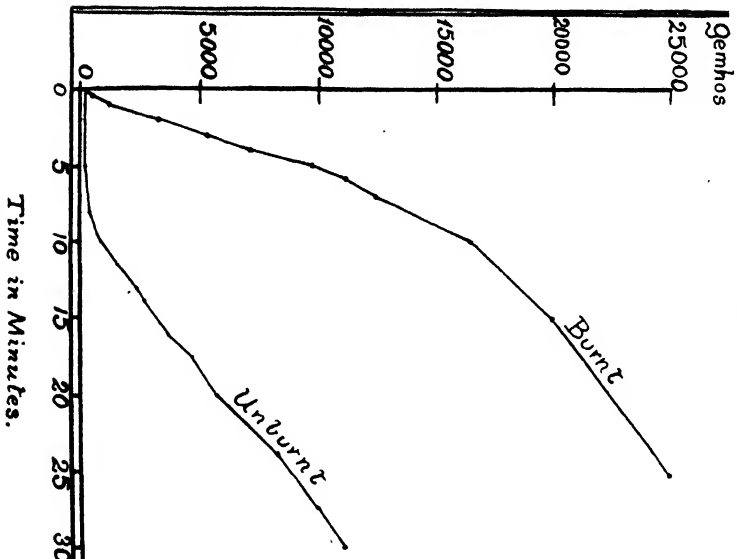


FIG. 3. Results of experiments on the rates of drainage of water and salts through burnt and unburnt soils. The first part of the experiment is not plotted. II shows the greater rate of passage of salts through burnt than unburnt soil. III shows that when a burnt soil and an unburnt soil are impregnated with salts and then washed through with water the concentration of the drainings falls very rapidly in the case of the burnt soil as all the salts are very rapidly washed out, but that with the unburnt soil the conductivity remains high for a much longer time as the salts are less rapidly removed. (The drainings here are smaller in quantity.) For further explanation see text, pp. 59-62.

Table XIV. *Experimental results on the rates of drainage of water and salts through burnt and unburnt soils.*

(I) First extraction with tap water			(II) Rate of drainage with 1 % Tidman's sea salt solution			(III) Washing out of sea salt with tap water		
Time in mins.	Resistance of the drainings in ohms		Time in mins.	Resistance of the water receiving leachings in ohms		Time of collection of fraction (minutes)	Resistances in ohms of the successive fractions of the drainings	
	Burnt soil	Unburnt soil		Burnt soil	Unburnt soil		Burnt soil	Unburnt soil
1	690	515	0	10,000	10,000	$\frac{1}{4}$	20	—
2	660	525	$\frac{1}{2}$	2,060	—	$\frac{1}{2}$	20	—
5	660	550	1	880	10,000	$1\frac{1}{2}$	30	—
$6\frac{1}{2}$	670	—	2	300	—	2	—	20
10	665	720	3	190	—	3	70	—
13	640	—	4	140	—	4	120	20
15	650	880	5	110	10,000	5	195	20
20	650	—	6	90	—	6	240	—
25	650	—	7	80	—	7	288	—
40	—	—	8	—	3,220	8	340	—
50	(560 c.c. passed)	975	10	60	1,040	10	410	20
65	—	—	$11\frac{1}{2}$	—	630	12	470	—
74	—	980	13	—	430	15	535	30
82	—	990	14	—	360	20	600	—
86	—	990	15	50	—	20-25	—	220
95	—	990	16	—	260	25-30	—	400
107	—	1030	$17\frac{1}{2}$	—	210	60-65	—	640
117	—	1030	20	—	170	—	—	—
—	—	(650 c.c. passed)	24	—	120	—	—	—
—	—	—	25	40	—	—	—	—
—	—	—	$27\frac{1}{2}$	—	100	—	—	—
—	—	—	30	40	90	—	—	—
—	—	—	—	(360 c.c. passed)	(155 c.c. passed)	—	—	—

allowed as much salt to be washed through in six minutes by 72 c.c. as the unburnt soil in 30 minutes by 155 c.c. (viz. enough to bring down the resistance to 90 ohms). It therefore appears to be about five times as efficient in allowing salt drainage, so far as rate is concerned, and to require less than half the amount of water to remove the same amount of salts.

The third part of the experiment, dealing with the washing out of the salts contained, shows that the rate of washing from the burnt soil is about 50 times the rate from the unburnt soil, the percentage increases in conductivity over given equal intervals (e.g. the first 15 minutes) being respectively 50 per cent. for the unburnt soil and 2675 per cent. for the burnt. The time required for the first signs of change in conductivity in the case of the burnt soil is also only a tenth of what it is for the unburnt, so that it may be safely concluded that leaching and drainage on slopes in nature are considerably facilitated by burning.

THE SOIL PROPERTIES OF SPECIAL ZONES AND IN RELATION TO
SPECIAL ECOLOGICAL FEATURES.

The relation between the properties of the soil and the ecological characteristics of the vegetation growing upon it are brought out by Table XV which has been constructed from the analyses of several soils from each type of zone, each soil being analysed in three different years and the results averaged together. The method of making these averages should preclude the possibility of the differences in the figures being due to seasonal variations or other irrelevant causes. The figures explain themselves and the table is easily read but attention may be drawn to one or two of the points which it shows. Fritsch and Salisbury (10) have pointed out that some years after firing the vegetation normally attains a phase in which *Calluna*, *Ulex nanus* and *Erica* are simultaneously dominant. This may be taken to be the average condition of the heath and is extensively represented. (It will be alluded to here, as in Fritsch and Salisbury's paper, as *C.U.E.*)

Table XV. *Averages for soils from special zones.*

Zone	Water content		Hygroscopic moisture		Humus		pH		Total salts		Coefficient of humidity	
	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"	2"	9"
Average <i>Calluna</i> - <i>Ulex-Erica</i>	18.7*	8.16	4.3	1.3	14.2	2.2	3.42	3.9	3825	1455	1.3	3.3
	(65)*	(57)	(48)	(49)	(50)	(48)	(38)	(39)	(63)	(63)	(65)	(57)
<i>Vaccinium</i> (7)†	43.3	7.2	5.1	3.7	36.0	2.2	3.2	3.5	7879	1383	1.2	3.3
<i>Molinia</i> (7)	42.7	12.4	5.8	3.4	24.1	12.6	3.30	3.36	5881	2144	1.8	1.0
<i>Aira</i> , 25 B (2)	10.4	8.3	2.3	1.6	4.7	1.5	3.5	3.7	2162	1525	2.2	5.5
Burnt areas on west side of Valley B with:												
<i>Ulex nanus</i> (3)	5.4	5.1	1.8	0.6	3.7	1.0	3.3	3.7	1793	750	1.5	5.1
<i>Erica cinerea</i> (3)	7.1	2.0	1.9	0.2	13.4	5.3	3.0	3.8	3159	1427	5.3	3.8
<i>Pteris</i> <i>aq.</i> (3)	19.7	3.9	4.4	0.4	5.6	1.7	3.4	3.6	4765	1715	3.5	1.9
Poor <i>Calluna</i> (25 O-Z) (1)	2.3	—	0.1	—	4.0	—	2.9	—	1368	—	0.6	—
<i>Erica tetralix</i> (4)	21.2	14.7	2.4	2.9	11.5	5.2	3.3	3.8	3466	2700	1.8	2.8
Gravel (4-5 J) (2)	11.1	11.8	2.2	2.1	2.0	1.7	4.0	3.8	1795	1880	5.5	6.9
Burnt areas	8.0	7.8	0.65	0.9	8.6	1.9	3.5	3.65	2664	864	0.9	4.1
	(24)	(4)	(24)	(4)	(24)	(4)	(16)	(4)	(24)	(4)	(24)	(4)

* The values are based on all appropriate samples taken in 1921, 1922, and 1923, the number of determinations which have been averaged being given by the figures in brackets in each case.

† Figures in brackets in this column apply to the whole line.

Table XVI. *Figures taken for comparison from paper by H. Jeffreys (16).*

	Water content	Humus	Coefficient of humidity	Acidity as given (= c.c. N/10 acid/100 gm. soil)	Acidity expressed as pH of 50 gm./20 c.c. extract
<i>Callunetum</i>	60.7	25.3	2.4	4.94	2.91
<i>Pteridetum</i> (1)	17.0	7.0	2.4	1.6	3.4
(2)	21.4	6.7	3.2	1.8	3.35
<i>Molinietum</i>	77.1	12.2	6.3	2.86	3.15

The first row of figures (Table XV) is for such average *C.U.E.* and is based on a fairly large number of samples, the numbers of readings used in obtaining the means being given in brackets. The readings for special zones may all be compared with these means in deciding whether they are abnormally high or abnormally low in any particular respect.

Soils on which *Vaccinium* is a prominent feature are characterised by being very rich in surface humus and soluble salts and possessing a high water content, but whether the high water supply or the richness of the soil is the more important factor there is nothing to suggest. *Vaccinium* is tolerant of a high degree of acidity, being associated with soils which are unusually acid both in their 2-inch and 9-inch depths, the respective *pH*'s being 3.2 and 3.5. It is more so apparently than any other species mentioned with the exception of *Erica cinerea*. *Vaccinium* can support an acid soil provided it be very wet but *Erica* will become dominant on a still more acid soil when the water content is very low. The figures for *Erica* in the table are those for a specially well marked zone on the west side of valley A. The valley slope here had been burnt in 1920 and showed in 1921, 1922 and 1923 along this side three very obvious, well-marked and distinct zones, the boundaries between them running at right angles to the direction of the valley, of which the first was dominated by *Erica*, the second by *Ulex nanus* and the third by *Pteris*. In each case the dominant constituted quite 80–90 per cent. of the vegetation in the three years mentioned though they were becoming less marked in 1924. Similar zonations were observed here by Fritsch and Parker in 1913 and are figured in Fig. 1 of their paper (9). The figures for each of these zones are recorded in the table (XV) as burnt areas with *Erica*, *Ulex nanus* and *Pteris* respectively. The zone with dominant *Erica* shows with one exception for its surface layers the most acid mean *pH* in the table, though the 9-inch depth is almost as alkaline as any. In this *Erica* zone then there is a greater difference between the acidities of the 2-inch and 9-inch depths than in any other situation and the fact, though it does not go in any way to explain the zonation, is probably significant in connection with the rooting depths of the plants concerned. *Erica* as shown by Fritsch and Salisbury (10) is comparatively shallow rooting, but in the case of the zones dominated by plants which penetrate more deeply such as *Ulex nanus* and *Pteris* there is a far less marked difference between the acidities of the 2-inch and 9-inch layers. There is least difference in acidity with the *Pteris* which penetrates most deeply. Of the three zones the *Erica* is the most acid, the *Ulex nanus* next and the *Pteris* zone the least, but the salt and humus contents do not run in the same order. In the case of the "*Erica* slope," for which figures have already been given in Table XIII, the degree of acidity is slightly less and the water content considerably higher.

Definite *Molinia* zones appear to be characterised by high acidity

($pH = 3.5$) and to be almost as acid at the 9-inch depths as at the 2-inch (mean $pH = 3.36$), in which feature they stand apart from all other cases. This is evidently related to the fact that the soils are altogether very rich in humus and that the 9-inch depths are particularly exceptional in this respect. If the figures for the *Molinia* zones in Table XV be compared with the average value of the two years means for valleys in general given in Table VII d, which here will form the fairest "control" for comparison, it will be seen that the water contents, the total salts and the 2-inch humus are large but all very close to the mean values for valleys, but that the 9-inch humus content is 12.6 per cent. against a mean value of 3.8 per cent., or over three times the normal. This probably explains the exceptionally high acidity at the 9-inch depths as compared with the 2-inch, and is evidently related to the fact, to which attention is drawn by Jefferies (14), that *Molinia* penetrates deeply into the sub-soil and possesses root hairs at all levels, so that more than the average amount of humus would be formed in the deeper layers. The coefficients of humidity are decidedly less in the *Molinia* zones than the average values for valleys, not apparently because there is a smaller water content but because there is more humus (cf. "sponge-like" action of the humus referred to above, p. 47). It is also to be remembered, however, that some of the *Molinia* zones were not actually in valleys, so this comparison with valley means, though useful in a general way, may not be altogether just.

The results for *Molinia* zones fall well into line with the observation of H. Jeffreys (16) that "*Molinia* usually grows where there is a large amount of humus in the soil and the water supply is peaty in character," but whereas Jeffreys found the Callunetum to possess a still higher acidity than the Molinetum, in the present case the reverse is true. It is interesting to compare the figures for the water content, humus, coefficient of humidity and acidity of the general *C.U.E.* vegetation and *Molinia* and *Pteris* zones with some of those given by Jeffreys. Some of the latter are quoted in Table XVI. Jeffreys' results for acidity were found by titration and given in c.c. of $N/10$ acid per 100 gm. soil, so, for the purpose of rendering them roughly comparable with the writer's results, they are in Table XVI also converted into the pH values which would have been given by a 5 gm. : 20 c.c. extract, assuming the acid to be completely dissociated. (This assumption is not strictly legitimate owing to the weak nature of the acids concerned, but will serve for a rough comparison.) Comparison of Tables XV and XVI shows that although the formations studied by Jeffreys were all much wetter than those of Table XV, the Callunetum in particular being also much richer in humus, some of the results are strikingly similar. In the *Molinia* zones the pH 's compare as closely as 3.15 and 3.3, and the humus contents found by Jeffreys fall between the 2-inch and 9-inch values recorded by the writer. The Pteridetum also agrees very closely, the typical water contents being 17 and 21 per cent. against 19.7 per cent., the humus 7 and 6.7 per cent. against 5.6 per cent., the co-

efficient of humidity being 2.4–3.2 against 3.5 and the acidities identical at a *pH* of 3.4. Salisbury, however (25), finds in the case of woodlands on Hythe beds (like the present soils) a *pH* for *Pteris* of 4.9 and for *Vaccinium* of 4.4 against the present record of 3.2.

Soils from the *Molinia* zones frequently showed evidence of peculiar properties during the determination of their acidities. The extract has the capacity of frothing very much like a solution of egg albumen so that a row of films is formed by the bubbles of hydrogen passing through the electrode vessel. Another peculiar property is that the solutions from these zones, after coming to a sort of transitory equilibrium on saturation with hydrogen and giving a *pH* reading of a normal order, were found to possess the capacity of “creeping” up to a higher and higher *pH* if the passing of hydrogen were much prolonged. Some of the *Molinia* zone solutions would creep in this way until showing an E.M.F. which corresponded to a *pH* of 9 or even 10 but nothing could be made out concerning the cause of the phenomenon. It was certainly due to some special substance or substances present in the soil extract and was not an artifact, since every possible precaution was taken and the phenomenon was persistently exhibited with different electrodes, different sources of hydrogen, different extracts of the same sample and so on, but the nature of the substances which cause it has not been determined. Bicarbonates might cause a slight creeping through washing out of CO₂ but could not account for an effect of the order observed. The effect was only exhibited with extracts from definite *Molinia* zones (e.g. those round 20 C, 19–20 C and at point O), except that it was also found in soils from gravel patches at 4–5 J, one soil from near the junction of the valleys A and B close to a definite *Molinia* zone, and a position in the *Erica* zone on the west side of valley A, in all of which localities *Molinia* occurred to some extent. Other samples estimated alternately with them came quickly to a final equilibrium in the normal way. The apparent association of the phenomenon with *Molinia* may of course be only incidental but seemed worthy of record.

In the case of the *Aira* (*Deschampsia*) zone for which figures are recorded in Table XV the peculiarities must be found by comparison with the figures given for Middle Line tops in Table VII. These figures were obtained from soils in topographically comparable situations. *Aira* (*Deschampsia*) *flexuosa* is of restricted distribution on the heath and is seldom abundant, but becomes a prominent feature in this particular zone at 25 B. By comparison with the control mentioned above it will be found to be relatively poor in humus and salts and to be below the mean acidity.

Erica tetralix forms well defined zones in certain places on the heath, the most remarkable being at 0 B and in the region of 3 J where it thrives almost to the exclusion of everything else. The soil is of more than average acidity in the surface layers but like that of the *Erica cinerea* zone of valley A already mentioned is almost as alkaline as the average at the 9-inch depths. As

already suggested this may again be associated with the relatively shallow rooting. The content in soluble salts is also exceptionally high for the deeper layers.

Special zones of *Triodia decumbens*, which is also of very restricted distribution, occur on the heath but so far as all that have been sampled are concerned they coincide with those of *Erica tetralix*.

At the end of the table (XV) figures are given for almost bare gravel patches on the land-slides at 4-5 J (see map) and for freshly burnt areas. The properties of burnt areas have already been fully discussed but the figures are interesting for comparison. The surface soil is less acid than that of any of the others except the bare gravel which is the most alkaline of all. Its frequent early colonisation by *Molinia* (cf. Fritsch and Parker (9)) therefore becomes at first rather surprising since *Molinia* is normally associated with high acidity. This, however, appears to be rather a manifestation of tolerance than of preference and the association of *Molinia* with lower acidity when not in a definite somewhat marshy "*Molinia* zone" is also well seen in its distribution along the 4 line (see Table II a), where it will be seen to coincide with the least acid zones. T. A. Jefferies (14) also observes that *Molinia* has a varied habitat, being associated with acid soils but also occurring in low-lying fens which are calcareous or neutral. It is therefore evidently tolerant of a wide range but in the present case is only associated with lower acidity when there is relatively little competition. It is at first a little surprising perhaps that the 9-inch layers of the bare gravel should be more acid than a corresponding depth of a soil bearing average *C.U.E.* The fact can only be attributed to the circumstance that the gravel, being nearly bare, is not subject to fires, so escapes their influence in periodically replenishing the supply of bases and reducing the acidity. It is of course also subject to the reception of acid drainings from *C.U.E.* higher on the slope.

The "Poor *Calluna*" zone at 25 25 Z is a small area which has stood out for many years as a zone of extremely poor vegetation, on which the soil has never become fully covered and bears practically only very poor *Calluna* plants which rarely exceed 5-6 inches in height. It will be observed that it is very poor in humus and especially in colloids as shown by the air-dry water content. It is also very poor in salts and the acidity is extraordinarily high (2.9). The reason for these characteristics is not apparent.

Bare patches. It has been observed that on fired areas definite bare patches may persist for many years after all the surrounding soil is again completely covered with vegetation. Samples have accordingly been taken from such bare patches and from under the surrounding vegetation with a view to determining the differences to which they are due. Only two sets of determinations have been made in this direction and these are given below but it cannot be said that they shed very much light on the question. The bare

patches appear in the aggregate to be more acid than the surrounding soil though possessing less humus and being less rich in salts, but the results are not at all definite and too few determinations have been made.

	Salts	pH	Humus
Bare patches	{1490	3.4	9.4
	{2325	3.3	7.8
	{3275	3.4	44.2
Controls	{1018	3.65	7.6

ANALYSES FOR POTASSIUM AND ALUMINIUM.

In a few cases potassium and aluminium were estimated with the object of determining the relative amounts of soluble potassium on burnt and unburnt ground and on the tops and in valleys and of finding out whether the aluminium content bore any relation to the degree of acidity. Estimations were made on four samples from tops and on five from valleys, but the results were not sufficient to lead to any conclusions. The figures showed no relation between acidity and aluminium content, nor apparently does any relation exist between the contents in either potassium or aluminium and topographical position. An attempt has been made already by Burgess (4) to correlate aluminium contents and acidities in acid soils, but whereas some parallel could be observed when the soils were taken in groups, the mean aluminium content (388 ppm.) of soils with a pH more acid than 5 being greater than that (26 ppm.) of soils with a more alkaline pH than 5, there was, as here, no regular parallel in the individual cases. The percentages of potassium average roughly the same both for tops and valleys and in the main run parallel with the percentages of humus. If any of the soils investigated had been sampled at very short intervals after firing, for reasons already put forward under the effects of fires, it seems probable that even this rough relationship would not have been obtained.

SUMMARY

A systematic soil survey has been undertaken of the area on Hindhead Common indicated in the accompanying map and defined by Fritsch and Parker (9).

Samples were taken at 100 feet intervals along certain transects across the area, and from certain special zones of which the vegetation showed characteristic features, and were analysed for humus, water content, hygroscopic moisture, acidity, calcium, nitrates, total salts and in a few cases aluminium and potassium.

The paper deals with the effects of wet and dry seasons, leaching and drainage effects on slopes, the effects of fires, leaching on burnt ground, the process of recovery from burning, the alterations in some physical properties of the soil on burning and the soil characteristics of special ecological zones.

The first characteristic of the soils in general is their very high acidity, the mean pH for an extract of 5 gm. soil in 20 c.c. of water being 3.4 for

2-inch depths and 3.9 for 9-inch depths. The 9-inch depths are almost invariably less acid than the 2-inch. The range of pH is 3.9–2.3 for 2-inch depths and 4.7–3.1 for 9-inch depths.

In dry and wet seasons the greatest variations in the coefficient of humidity are found in surface layers on high ground and the least variations in surface layers in the valleys. The 9-inch depths are intermediate, the tops again varying more than the valleys. On old ground a wet season leads to a loss of salts by the tops and a considerable gain in the valleys. 9-inch layers, however, do not gain at the expense of the 2-inch layers.

Fires lead to the destruction of 60 per cent. of the original humus in relatively young heath but only about 30 per cent. in older heath, where the soil is particularly rich in humus. The colloidal properties of the organic matter which remains are always much impaired. Drainage of salts into the valleys becomes more pronounced, and the 9-inch layers in the valleys at least do now show a considerable increase at the expense of the salts lost by the high ground and surface layers. The total salts are at first increased but are then rapidly leached out until well below normal. They continue to fall through further leaching until a late stage in recolonisation (possibly for six to eight years), when sufficient new humus is formed to check the process. The valleys are probably more hospitable for recolonisation through their higher salt content gained by this drainage. The acidity is always decreased by a fire and owing to the equalisation of texture becomes more similar at the 2-inch and 9-inch depths.

During recovery from burning there is a gradual increase in humus and acidity and lastly in salts. The increase in acidity is more rapid in the valleys, so that the bottoms of the slopes come again to be considerably more acid than the tops. A factor aiding the production of relatively high acidity in the valleys may be the reduction in the ameliorating drainage effects through the greater accumulation of humus.

A method is developed for the quantitative evaluation of the extent of leaching and drainage effects on slopes as shown by the changes in the ratio of salts to humus at different levels.

Laboratory experiments show that water and salts pass more readily through burnt than unburnt soils and that absorption of salts is diminished by burning. A greater loss by leaching and drainage would therefore be expected on burnt than on unburnt areas. This is found in practice.

The soil characteristics of special ecological zones such as areas dominated by *Erica tetralix*, *Ulex nanus*, *Pteris aquilina* and *Vaccinium* or in which *Molinia* or *Aira (Deschampsia) flexuosa* become prominent features are briefly discussed and can be gathered from Table XV.

The results for certain zones of poor vegetation, gravel and bare patches, and concerning the distribution of potassium and aluminium are also given in the text.

In conclusion my thanks are due to Professor Fritch, both for the facilities offered me and for his advice and criticism. I am also much indebted to Dr Salisbury, who has been occasionally troubled for the sake of his helpful suggestions, and to many of the advanced students of this Department, who have been of great assistance to me both in the laboratory and in the field. Lastly, many thanks are also due to Mr W. A. Glanville, formerly of the Engineering Department here, who has carried out a special survey of the Heath and prepared an accurate map of the paths and contours, a copy of which has been used in the preparation of Fig. 1.

LITERATURE

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EPHARMONIC RESPONSE IN CERTAIN NEW ZEALAND SPECIES, AND ITS BEARING ON TAXONOMIC QUESTIONS

BY H. H. ALLAN.

(*With twelve Figures in the Text.*)

A. INTRODUCTORY

The development of genetics and of ecology in recent times is reacting strongly on taxonomy, and will have a more and more profound influence as accurate knowledge of organisms in the field and in the experiment garden increases. The problems of variation and the delimitation of species are being viewed from new angles, and systematic work is becoming increasingly coloured by the new conceptions, while the effect upon evolutionary speculation is no less evident.

New Zealand floristic botany has been dominated by the conceptions of that *princeps botanicorum*, Sir J. D. Hooker, but admirable as are the floras produced under his inspiration it is becoming clear that a vast amount of intensive work lies before the taxonomists of the future, now that it is seen that variation cannot be accepted as a datum or put aside as a trifling matter, but must be analysed, as far as may be, according to its diverse causes. The dictum of Lotsy (20, p. 41), "inheritable variability does not exist," must be proved or disproved—it cannot be neglected. Hooker (18, p. viii), from his extensive knowledge of plants the world over, both wild and cultivated, living and stored in herbaria, was led to conceive of species as being widely spread and very variable. He says (*l.c.* p. xiii): "The result of my observations is, that differences of habit, colour, hairiness, and outline of leaves, and minute characters drawn from other organs than those of reproduction, are generally fallacious as specific marks, being attributable to external causes, and easily obliterated under cultivation. It has hence been my plan to group the individuals of a genus which I assume after careful examination to contain many species whose limits I cannot define, that the species shall have the same relative value as those have of allied genera whose specific characters are evident." As an illustration he takes *Blechnum capense* (*Lomaria procera*): "The resident may find two varieties of this and of many other plants, retaining their distinctive characters within his own range of observation (for that varieties often do so, and for a very uncertain period, both when wild and also in gardens, is notorious), and he may have to travel far beyond his

own island to find the link I have found, in the chain of forms that unites the most dissimilar states of *Lomaria procera*; but he can no more argue thence for the specific difference of these, than he can for a specific difference between the aboriginal of New Zealand and himself, because he may not find intermediate forms of his race on the spot" (*l.c.* p. xiv).

Following these lines of thought taxonomists dealing with New Zealand material have tended to unite groups which, however distinct their extreme members, are connected by a series of "intermediates," the species then being spoken of as "variable." Carried to its logical conclusion Hooker's view justifies the action of Mueller (21, cited in 4, p. 446) in grouping together all the Australian and New Zealand, and most of the South American, gentians under the one name *Gentiana saxosa*! The fact that we may find a form in South America that is a "link" missing in a chain of forms in New Zealand does not seem to prove anything, unless we know the causes operating in the two countries to produce the intermediates. Whether we give the Maori and the various types of Europeans in New Zealand varietal or specific status matters little. Intermediate forms are common enough, and the reason for them is well enough known! The finding of a race having intermediate characteristics in, say, one of the Pacific Islands would be interesting, but would not explain away the half- and quarter-caste.

However far from complete our analysis is, we now know that intermediates fall into several distinct classes. We have: (1) Aggregate species made up of a number of distinct microspecies—the Linneons and Jordanons of Lotsy (*l.c.* p. 27)—that remain constant when self-fertilised; e.g. certain varieties of *Hebe salicifolia* (11, p. 200). Into the vexed question of their origin, whether mutational or what not, we need not here enter. (2) Groups in which the intermediates are apogamous races, whether their origin be by hybridisation or not, e.g. certain forms of *Erophila verna* (22, p. 11). (3) Groups of intermediates due to hybridisation. These groups may be (*a*) inconstant forms, not breeding true, e.g. \times *Coprosma Cunninghamii* (2, p. 310), or (*b*) constant forms, breeding true¹. (4) Groups of intermediates due to epharmonic response to environment. Possibly in certain cases such intermediates may ultimately become constant, or certain of the forms may, as suggested by Cockayne (10, p. 25) for *Edwardsia prostrata*. (5) Groups in which individual differences occur that cannot at present be assigned to any known cause. In general, e.g., the juvenile form of *Aristotelia fruticosa* can be correlated with its environment as epharmonic, but the wonderful minute differences in leaves on individual plants defy analysis (Fig. 1). It is easy but not enlightening to speak of them as "fluctuating," "spontaneous," and so forth. When *A. serrata* occurs in company with *A. fruticosa* forms of the hybrid \times *A. Colensoi* will be met with, and the confusion becomes worse confounded.

¹ Such supposed "constant hybrids" need critical examination. The example of \times *Geum intermedium*, alleged by Blaringhem (3, p. 322) to be constant, is said by Weiss and Rosen (*Nature*, 4th Oct, 1924, p. 500) to show distinct segregation of characters in F 2.

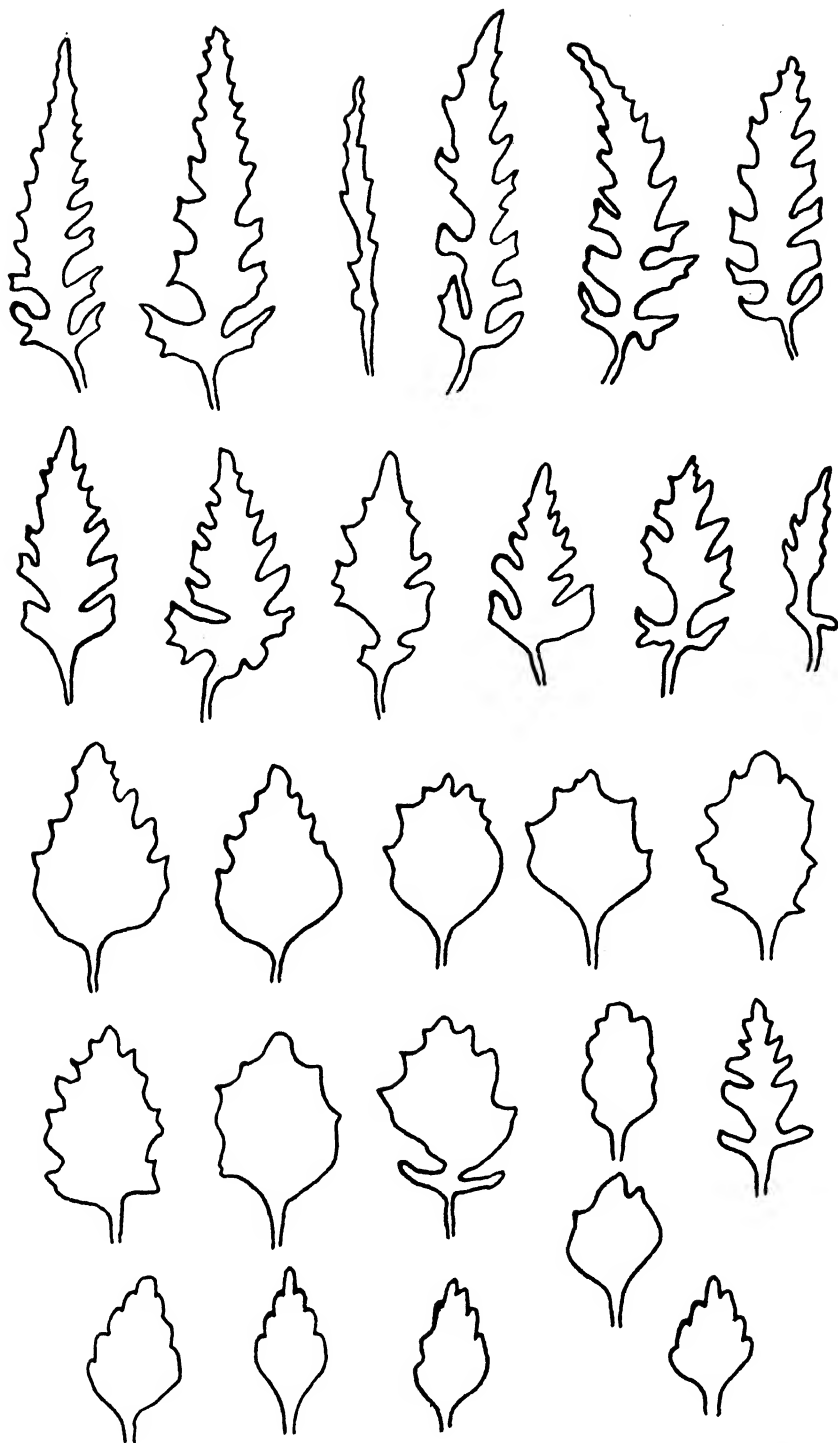


FIG. 1. Leaf-tracings of juvenile *Aristotelia fruticosa*. The leaves were irregularly placed on a single branch; forms on the lowest line approximate to those of the adult.

In nature these groups may be almost indissolubly entangled, but field studies supply many clues as to the most profitable lines of research in any particular examples of groups of intermediates met with, and it is no longer possible to rest content with a simple description of the polymorphy that exists, or with a statement that the species is very variable. And while Hooker's position as regards "links," and as to hybridisation (*l.c.* p. xv), is no longer tenable, it remains true that the essay of 1853 still repays careful reading.

Readers who wish to review the present state of our knowledge of these matters in the New Zealand flora, should consult Cockayne's important papers and books (6-16). It may, however, be well to indicate here the exact standpoint of Cockayne by citing certain of the principles laid down by him as a guide for the establishment of species or varieties (13, p. 161): "(1) The starting point in the setting-up of species is the individual. (2) Groups of individuals which resemble one another in every character and reproduce their like, subject, of course, to unfixed fluctuating variations, constitute specific units and may be designated 'microspecies.' (4) Two or more closely related microspecies may be united into a group for the sake of: (a) convenience in identification, (b) emphasizing the close relationship of minor groups (microspecies), (c) phytogeography. (5) Such a major group as constituted in (4) forms an aggregate or collective species. (15) In certain cases groups, otherwise well defined, seem to be united by 'intermediates' which cannot be joined to such groups or made into one or more species. Such 'intermediates,' according to the teachings of genetics, may be assumed to be hybrids between microspecies."

The following sections deal with certain examples of epharmonic response, roughly classified, that have come under my observation, and that bear on the questions raised in the introduction. The subject deserves extended study and would repay monographic treatment. I use the term epharmony to apply to all changes in the form of an organism traceable to varying conditions of the environment.

B. CHANGES IN LEAF SIZE, SHAPE AND TEXTURE

(a) *Ranunculus Monroi* var. *dentatus*. Kirk (19, p. 9) relies on the following leaf-differences in separating the variety: *R. Monroi*, leaves rounded reniform or nearly orbicular or ovate; crenate or crenate-dentate; glabrate or sometimes silky or villous—var. *dentatus*, leaves broadly ovate or ovate-lanceolate; crenate, lobed, or dentate; clothed on both surfaces with strigose ferruginous pubescence. Cheeseman (4, p. 12) accepts the variety, and only refrains from creating it a species owing to the "occurrence of numerous intermediates."

On Mt Peel, Canterbury, grows a plant referred to the variety, as a rock-plant from c. 950 m. upwards, descending along streams to much lower elevations. The changes in size and in the degree of tomentum on the leaves

is most striking, as shown in the following table. A complete series of inter-grading forms can be found according as the degrees of shelter, shade, root-room, and moisture change. Moreover I have produced similar changes in garden-grown specimens from the various habitats. Plants, also, taken from the rocks and replanted in a sheltered nook by a stream-side, grew in the course of two seasons into forms indistinguishable from those of plants growing naturally in the same spot. A plant intermediate between C and D of the table planted among the summit rocks grew into a form closely approximating to A.

Epharmony in Ranunculus Monroi Hook. f.

	Specimen from exposed rock-cleft c. 1300 m.	Specimen from sheltered rock-cleft c. 1300 m.	Specimen from stream- side c. 900 m.	Specimen from stream- side in shade c. 850 m.
	A	B	C	D
LEAVES	3-5 cm. by 2-3.5 cm. Coriaceous, broadly ovate, crenate Tomentum extremely dense; below of shaggy appressed ferruginous hairs, above of long pale hairs	5-8 cm. by 7-9 cm. Sub-coriaceous, broadly ovate, crenate Tomentum similar to A but less dense and paler below, above scattered long pale hairs	7-12 cm. by 7-10 cm. Rather fleshy to sub- membranous sub-ro- tund, cordate, crenate Tomentum below much less dense; pale below, above of only scattered hairs	10-13 cm. by 8-11 cm. Thin and membranous, similar to C, but larger and more irregular Tomentum reduced to very scant hairs below, glabrous above
PETIOLES	1-3 cm. Densely clothed with ferruginous hairs; sheathing-base 0.3- 0.5 cm. by 1.5-2 cm.	4-7 cm. Similar to A; sheathing- base 1-1.5 cm. by 2-2.5 cm.	7-16 cm. Similar to A; sheathing- base 1-2.5 cm. by 3-5 cm.	10-20 cm. Rather densely clothed with brownish hairs to glabrate; sheathing- base 2-3 cm. by 3-6 cm.
SCAPES	7-9 cm. Simple or once-branched tomentum dense, pale brown	15-20 cm. Sparingly branched to- mentum similar to A	15-30 cm. Several times-branched tomentum less dense	20-40 cm. Much-branched, sub- corymbose tomentum reduced to sparse pale hairs
BRACTS	0.5-1.5 cm. Linear to linear-lanceo- late	1-3 cm. Linear, lower slightly lobed	3-4 cm. Lower deeply lobed	5-6 cm. All except uppermost deeply lobed
SEPALs	6-8 mm. Dense pale-brown pu- bescence below	7-12 mm. Pubescence hardly dense, still paler	10-13 mm. Pubescence similar to B	10-15 mm. Pubescence reduced to scant pale hairs
PETALS	9-12 mm.	9-12 mm.	10-15 mm.	10-15 mm.

It will be seen that as far as the Mt Peel plants are concerned Kirk's points of difference fall to the ground, unless by variety we merely mean an unstable form. This does not prevent the possibility of *R. Monroi* being an aggregate species, but proves that herbarium specimens alone cannot settle such questions (Figs. 2, 3).

Similar inter-grading forms were observed in the case of *Senecio bellidioides*, some answering to the description of var. *glabratus* (19, p. 339), but clearly related to their environment. Some subalpine forms of *Anisotome aromatica* are only distinguishable from *A. imbricata* by the characters of the fruit. The var. *incisa*, of the former species, distinguished by its flabellate or rhomboid leaves, is certainly a microspecies, but I have been able to alter its leaf-



FIG. 2. *Ranunculus Monroi*, forms A, B, C of table.



FIG. 3. *Ranunculus Monroi*, form D.

characters considerably in moist-air cultures (Fig. 4). Other examples of extremely plastic species could be given, and it seems wiser in such cases to use the non-committal term "form" till such time as research has differentiated the microspecies from the unfixed epharmonic forms.

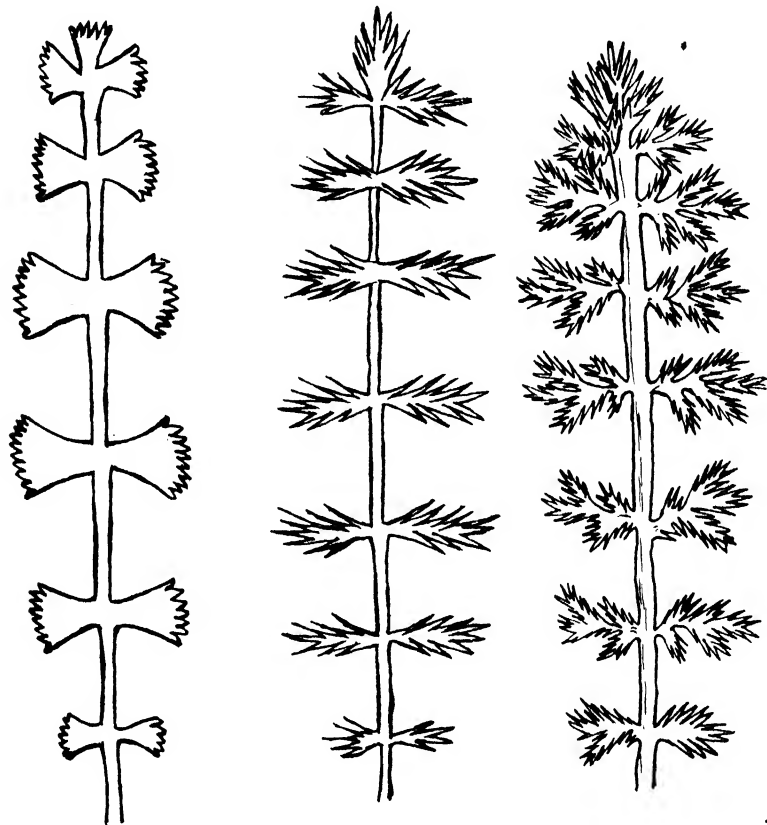


FIG. 4. Left—ordinary form of leaf of *Anisotome aromatica* var. *incisa*. Centre—leaf from same plant after cultivation in moist air. Right—leaf of typical *A. aromatica*. All $\times 3$.

(b) *Plagianthus ribifolius*. A detailed account of the life-history of this species is given by Cockayne (6, p. 269). *P. Lyallii* has adult leaves ovate-acuminate, glabrous, with stellate pubescence on the mid-ribs and principal veins, while those of *P. ribifolius* are usually merely acute, and the stellate pubescence is not confined to the veins, the under-surface being covered with a dense mat of stellate hairs, the individual hairs longer than those of *P. Lyallii*. The distribution of the species is remarkable: *P. Lyallii* is apparently confined to regions of the South Island exposed to the great western rainfall; *P. ribifolius* occurs in the eastern mountain region, beyond the limit of western rainfall. Cockayne says (6, p. 272), "It is ecologically of extreme interest that a character seemingly so trivial as a slight variation in hairiness of leaf

has led to these two species not having intermingled, although they approach in places to within only three or four miles from one another at the most; and it shows, moreover, how an apparently unimportant character may govern the climatic distribution of a plant. It may also be pointed out that both forms thrive equally well side by side in lowland gardens where the rainfall is slight, and the characters of each, so far as I have been able to ascertain, remain unchanged."

Now *P. ribifolius* is a plentiful plant on Mt Peel, forming groves at elevations above the general forest line, and descending as occasional plants into the forest of the upper plains. The forest is true rain-forest, and the environment perfectly suited to *P. Lyallii*, but it does not occur. In dense shade by the sides of streams the Mt Peel plant, elsewhere typical *ribifolius*, becomes a shrub the leaves of which are almost identical with those of *P. Lyallii*, being much more acuminate, and having the pubescence practically confined to the veins. Rarely one finds specimens showing both forms of foliage. It would seem that research is required to determine whether we are not, after all, dealing with a species sufficiently plastic to adapt itself to the very different conditions of habitat in which the two forms grow. It may be that we have here an example of an epharmonic variation that has become fixed, or almost so, but the question as to the taxonomic status of the two forms seems still open.

(c) *Olearia capillaris*. This species is treated by both Kirk (19, p. 268) and Cheeseman (4, p. 285) as a variety of *Olearia arborescens*, the latter writer stating (5, p. 88): "the variety *capillaris*, although remarkably distinct in its extreme form, can be traced step by step into the ordinary state." As stated by Cockayne (16, p. 117) the "steps" are almost certainly due to hybridisation. *Olearia capillaris*, if that name be confined to the "extreme form," is a semi-divaricating shrub with leaves ± 7 mm. long, while *O. arborescens* is a bushy tree, with leaves ± 50 mm. long.

At the same time *O. capillaris* is remarkably responsive to environment. Whereas the adult has leaves 5–7 mm. by 6–8 mm., broadly ovate or sub-orbicular in outline, with sinuate margins, juvenile plants growing in dense forest shade are of open habit, sparingly branched, with much larger leaves, 18–30 mm. by 20–35 mm., having crenate-sinuate margins. The branches are often more or less prostrate and rooting. Where both parents occur, there will occur the hybrid forms, and the status of individual juveniles will become very difficult to determine. It is obvious that taxonomists have here a group that must be taken to the experiment garden to be discriminated (Fig. 5). Large-leaved juveniles growing in my garden are now producing leaves of adult size and form.

(d) *Olearia virgata*. This species has been described by both Kirk (19, p. 276) and Cheeseman (5, p. 19) as very variable, and several varieties have been created. It is undoubtedly a big and difficult aggregate group, one race



FIG. 5. Juvenile (lower) and adult (upper) forms of *Olearia capillaris*.



FIG. 6. (a) Normal and two reversion shoots of *Olearia virgata* var. (North Island).
(b) Lower-grassland form of *Olearia virgata* var. (South Island). Upper—forest form of same var.

of which has been segregated by Cockayne (9, p. 173) as *O. lineata*, a course which field evidence strongly supports, and further segregations will certainly be made. Nevertheless certain forms are very plastic, and the epharmony of the aggregate requires investigation before an intensive treatment can be satisfactorily carried out.

In the rain-forest climate of Feilding, North Island, a very distinct-looking form grows as a forest-margin plant of rather densely divaricating habit. It is also prominent in certain swamps. The leaf-blade is coriaceous, quite flat, or the margins minutely recurved. The leaves are glabrate above, and clothed in dense, appressed tomentum below. They average 3 mm. by 6 mm., with petioles of 2 mm. One rather large specimen, growing under trees of *Leptospermum ericoides*, had been cut down and was regenerating from the base. The shoots were erect, sparingly branched, and the leaves thin and flat, averaging 8 mm. by 16 mm., with petioles up to 12 mm. The upper surfaces were glabrous, and the lower only thinly pubescent. A cutting from this has reverted in my garden in a single season to a widely divaricating form with leaves precisely similar to that of the ordinary form (Fig. 6, a).

C. IN-ROLLING AND FLATTENING OF LEAVES

(a) *Olearia virgata* var. A distinct microspecies from the one referred to above is common in the tussock-grassland and swamp at Mt Peel. It is a rather densely divaricating shrub with branchlets slender and clothed with dense white pubescence. The leaves have strongly recurved margins, so that they become linear and semi-terete in gross outline, resembling but much shorter than those of *O. lineata*. They are collected mainly in opposite fascicles on short arrested branchlets, are dark green above with many rather long soft hairs, and are densely covered below with white tomentum, among which are numerous scattered long hairs similar to those of the upper surface. The average measurements are 1.5 mm. by 7 mm., with petioles 2 mm. When forced flat the blades are 3 mm. wide.

Plants are occasionally met with growing in forest shade a little way from the margin. The effect of the environment is to give the plant so different an appearance that it was considered by a prominent New Zealand taxonomist to be an undescribed species, till specimens were obtained showing that it was another case of unfixed epharmonic response. The branches lose their divaricating habit, and the plant becomes a lax open shrub with scanty pubescence on the branchlets. The leaf-bearing branchlets lengthen out, separating the opposite pairs of leaves, which become perfectly flat and average 8 mm. by 17 mm., with petioles of 3 mm. The upper surfaces carry few or no hairs, the pubescence beneath becomes thinner, with only few scattered long hairs. The leaf-tip becomes minutely apiculate, instead of merely acute.

Specimens were found on the adjacent grassland showing every gradation of leaf-form and size. These plants were surrounded by a dense growth of

tussock-grasses and *Blechnum capense*. Shoots growing amidst the grass and fern had leaves identical with those of the forest form, and were succeeded above by a series becoming gradually smaller and more recurved as the branches reached above the surrounding vegetation, till the uppermost parts of the shrubs assumed the divaricating form of the open grassland. Plants of the latter form cultivated under shade changed into that of the forest (Fig. 6, b).

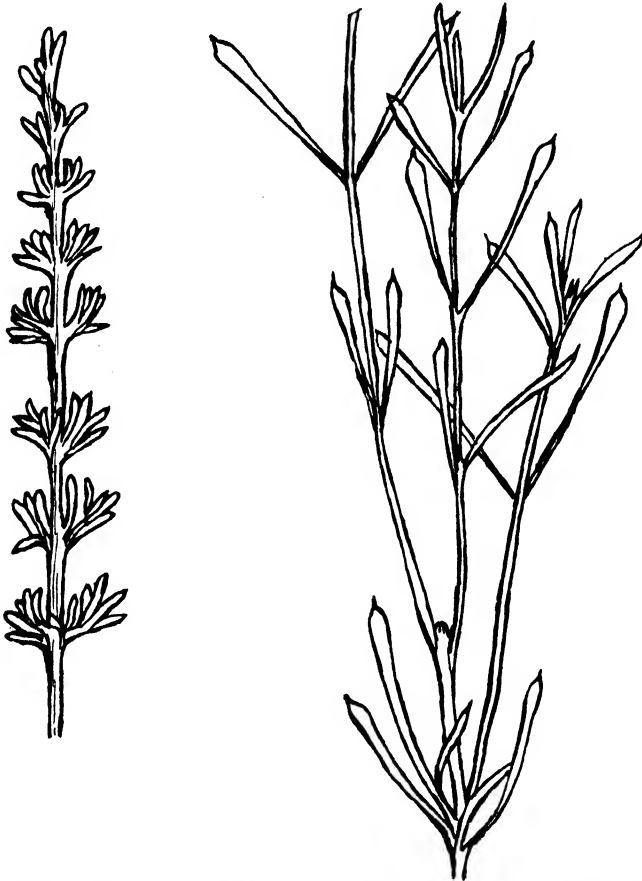


FIG. 7. Left—normal shoot of *Olearia Solandri*, $\times 2$. Right—reversion shoot from same plant, nat. size.

(b) *Olearia Solandri*. This species, similar in many respects to *O. virgata* but of different habit, is marked by the golden tomentum of the branchlets. The tomentum of the under-surface of the leaves is also said to be pale yellow, but it is white in all specimens examined by me. This yellow tomentum is often very deep toned in seaside plants, but is paler on inland ones, and is also less viscid. The leaves are linear or linear obovate, with mid-ribs prominent below and much recurved margins. They average 5 mm. in length, including

the petiole. Plants growing in the shade of *Leptospermum* thickets have rather larger leaves, less recurved, and with thinner tomentum. The colour of the branchlets is very much paler. Reversion shoots may sometimes be found near the base. These are slender, erect, with thin white tomentum. The leaves are flat with very thin white tomentum below, and average 20–30 mm. in length (Fig. 7).

(c) *Paratrophis opaca*. This species was accepted by Cheeseman with considerable hesitation (4, p. 633) as intermediates exist between it and *P. microphylla*. The former has leaves ± 10 cm. long, the latter ± 2 cm.



FIG. 8. Normal and rolled-leaf forms of *Paratrophis* from the same plant.

and with a distinct juvenile small lobed-leaf form. The intermediates are almost certainly hybrids, but there is considerable reduction of size in leaves of *P. opaca* on trees growing in exposed situations. The form illustrated (Fig. 8) is probably a hybrid. Sheltered leaves are ± 3 cm., thin in texture, flat; leaves on the upper part of the shrub, exposed to salt gales, are of the same size, but more coriaceous, with the margins much recurved, often right to the mid-rib. They are also sub-erect on the branchlets, not spreading. I have observed only the one plant of this form showing leaves both flat and recurved, but in the same locality—Titahi Bay, west coast north of Wellington

—a similar recurving was noticed on specimens with leaves nearly approaching those of *P. opaca* in size.

In these cases the leaf-inrolling is unfixed, the plants responding directly to the changed conditions, but in the case of *Olearia nummularifolia* and *O. cymbifolia* it is possible that an originally epharmonic change has become fixed. The latter differs from the former in having much recurved leaf-margins, and is treated as a variety of *O. nummularifolia* by both Kirk (19, p. 273), who suggests that it “appears to be a depauperated condition, largely caused by the ravages of insects,” and Cheeseman (4, p. 290), who speaks of its distribution as local.

Cockayne has been able (14, p. 72) to flatten the leaves in moist-air cultures. He also considers (16, p. 127) that hybrids between the two occur wild. Evidently further work is desirable on these two species.

D. THE ASSUMPTION OF THE LIANOID HABIT

(a) *Senecio sciadophilus*, a species occurring in a few scattered localities in the South Island, is of interest from the varieties of habit it assumes, though it raises no taxonomic difficulties. The following description is drawn up from observations at Mt Peel. The seedling has leaves spirally arranged, tri-lobed, or rarely tri-foliate, with the toothing of the edges less marked than in the adult. The slender stem may commence twining if situated near a slender support, but more commonly flexes over and grows along the ground, with ascending tip. The leaves then formed have the orbicular, coarsely toothed adult form, and the spiral arrangement becomes obscured by the twisting of the petioles. The stems branch freely, root at the nodes, and form a loose mat. The branches grow over logs or low shrubs in a tangled mass, or if the bush is taller ascend in a slightly twining manner and form a scrambling cover to the shrub. Long semi-erect shoots grow out, and, meeting a suitable support twine vigorously, or, failing support, incline over and are added to the general mass. Such shoots may even again reach the ground and take root. Short side shoots grow erect and bear the flowers. The twining is both sinistrorse and dextrorse, the former being more common, and these shoots may reach to the top of tall shrubs, there again to develop a scrambling mass of flexuous stems (Fig. 9).

(b) *Fuchsia Colensoi* is one of the “very variable” species of the floras. Much of the polymorphy can be traced to hybridisation with the tree, *Fuchsia excorticata*, but there are also probably distinct microspecies, and there may well be, as suggested by Cockayne (10, p. 21), climbing and non-climbing races. The form found at Feilding, which I have briefly described elsewhere (1, p. 403), is always a scrambling liane, there being no intermediates where *F. excorticata* is absent. The plant when growing in the open forms mounds of interlacing stems, thus agreeing exactly with the behaviour of species of *Rubi*,

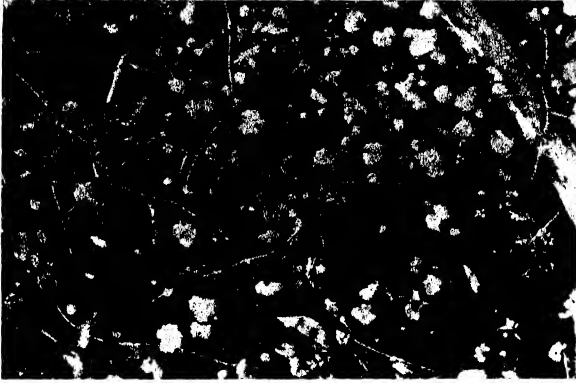


FIG. 9. The liane *Senecio sciadophilus* as a loose-mat-forming floor plant.



FIG. 10. Prostrate form of *Coprosma propinqua* var. on shingle beach.

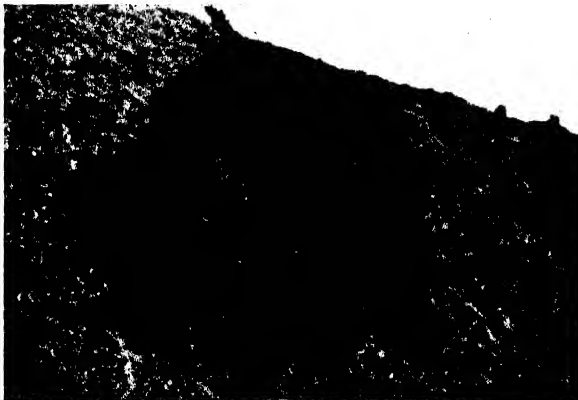


FIG. 11. Densely divaricating form of *Coprosma propinqua* var. on open hill-side.

as described by Cockayne (10, p. 22), and differing from the South Island twiggy shrub of the grasslands.

(c) Certain herbs. *Lobelia anceps* assumes a variety of forms consonant with its habitats. The salt meadow plant is usually suberect, rather stout, with rather large succulent leaves. Growing on banks and cliffs it becomes prostrate or drooping, and with suitable substrata the stems root freely at the nodes. Inland forms are more slender with thinner leaves. Growing under shrubs the plant may be met with as a small scrambling liane with weak slender stems up to 1 m. long and very sparingly branched. Field studies thus suggest that we have one very plastic species, and not a series of microspecies, but experimental study is required.

Stellaria parviflora. This is usually a small diffuse herb of the forest-floor, sometimes, however, forming dense matted patches. At the forest margin I have noted it assuming the lianoid form on shrubs and small trees. The ascending tips of the stems turn up through twigs and the internodes elongate. Slender side branches droop from these and help as supports, while short roots are given off at the nodes and may ensconce themselves in crevices and afford a firm support. The tallest example I have noted reached over 1 m. high, but usually it is much shorter.

Acaena Sanguisorbae. Several varieties of this aggregate are able to become small lianes. In its usual growth-form the species is a creeping and rooting semi-woody plant forming loose mats. In rain-forest climates the plants, when growing amongst small bushy shrubs, become lianoid, the tips of the stems growing up through the branches as searcher-shoots. On reaching the upper part of the bush these stems branch, scramble over the shrub, and may again incline downward and take root. Such stems are often ± 2 m. in length, with sometimes abortive roots at the nodes.

The case of the exotic grass *Agrostis tenuis* may be mentioned, its behaviour resembling that of *Acaena Sanguisorbae*, and occurring in similar situations. Sparingly branched stems over 2 m. long may be found growing over shrubs on the outskirts of forest.

E. THE CREEPING AND ROOTING HABIT

(a) *Myrtus pedunculata*. As pointed out by Cockayne (8, p. 19) *Myrtus pedunculata* and *Leucopogon fasciculatus* are examples of shrubs that have an erect bushy form, and also a prostrate one. In part such changes of form are unfixed epharmonic responses, but there are cases that are difficult to explain on this ground, and a critical study of the matter is much required. *M. pedunculata* is an aggregate species, there being very distinct varieties among the erect forms. It may well be that certain creeping forms are micro-specific. In the Southern Beech forest of North-west Nelson there occur patches several square miles in area composed of the decumbent stems of *M. pedunculata*, connected below by far-spreading, branching, horizontal

rhizomes. From these develop miniature thickets of erect bushy stems, the decumbent stems dying away. With the growth of the erect stems, and the dying out of some, open patches of shrubs are formed that could easily be



FIG. 12. Normal and shade leaves of *Coprosma propinqua* var. from the same plant.

mistaken for individual plants were the sequence not studied. In other forests erect forms occur in which no trace of a creeping habit can be found.

Cyathodes acerosa, too, may form open mats, or dense bushes, the two

forms sometimes growing alongside one another. The phenomenon seems much rarer in this species than in either *M. pedunculata* or *L. fasciculatus*, so far as my observations go.

A case that is certainly unfixed epharmonic response is that of *Helichrysum glomeratum*. This is usually an erect bushy shrub, but in dense forest shade, an unusual station, I have met it as a decumbent shrub, the long trailing branches rooting freely where they touch the ground.

(b) *Coprosma propinqua* var. Cockayne (7, p. 378) has described the epharmonic response shown by *C. propinqua* as a coastal plant. "This shrub, in its usual stations, such as lowland or subalpine scrubs and fresh-water swamps, is erect with numerous more or less divaricating branches. But when it grows on the coast . . . it is usually much 'wind-shorn' and frequently quite prostrate, being flattened against the rocks which emerge from the peaty ground, and clinging closely to their surface. But all transitions may be seen, from the wind-swept plant to the normal, and there is no reason to expect that the former form is in any way hereditary." I have been able to study these changes in a variety of *C. propinqua* growing on Kapiti Island. The prostrate form grows on the large shingle banks of the coast, and the stems do not strike root. Probably the insolation has much to do with the growth-form. On the lee sides of the shingle banks the plants are less prostrate, and on the forest margin are of ordinary divaricating form. Growing in the shade the plant becomes open with much larger leaves (Figs. 10, 11, 12). Cockayne, however, has shown (7, p. 379) that the prostrate form of the species growing on Chatham Island retains its habit even under cultivation in sheltered positions, and considers that there is here evidence as to fixation of acquired characters.

(c) *Hierochloa redolens*. The segregation of the microspecies of this aggregate is complicated by the presence of epharmonic forms. The following growth-forms were noted at Mt Peel. In the tussock-grassland the species is generally a robust semi-tussock grass, but when growing on the trunks of *Carex secta* in swamps, it is reduced to loose tufts. On steep moss-covered banks over which water trickles it is a tuft-plant with long flaccid drooping leaves. In the stretches of *Blechnum capense* on the open hill-side there is a form with well-developed rhizomes, the plant covering considerable patches.

F. FLOWERING JUVENILE FORM

Of the 200 or more species of New Zealand plants that have a juvenile stage very distinct from the adult, a certain number have been observed to flower both on the adult and on the persistent juvenile base, or on reversion shoots of juvenile form. *Dracophyllum longifolium* was observed by me to flower while still in the juvenile form. The differences between the juvenile with its long, spreading leaves, arching downward, and the adult with smaller, narrower, stiff, erect leaves, are very pronounced. Plants that invade the

upper forest margin from the lower subalpine shrublands at Mt Peel retain the juvenile form of leaf for long periods. The growth-form is no longer fastigiate, the plant becoming a shrub about 2 m. tall, with spreading naked branches, ending in rosettes of leaves of the juvenile form. In this condition the plant flowers and fruits freely. A taxonomist dealing with the two flowering forms, and not knowing the life-history of the plant, would certainly consider them two distinct species. *Pennantia corymbosa* also flowers while still in the juvenile stage, apparently rarely, though specimens flowering on the persistent juvenile base and on the adult portion are more commonly met with.

G. COLOURATION PHENOMENA

Very little work has been done in New Zealand on colouration as affected by environmental conditions, but although we have little suggestion of the beautiful autumn colouration of other lands there is much interesting material awaiting study by the ecologist and physiologist. Here a few points germane to this paper are noted.

(a) *Azolla rubra*. Plants of this species growing in shade have the leaves a beautiful sage-green. Such plants brought into the light rapidly turn the usual reddish colour. A number of other species could be cited showing similar epharmonic colour reactions, e.g. the bronzing of leaves of *Rubus subpauperatus* in winter, the purple colouration of *Agrostis subulata* in exposed subalpine stations. Not the least striking is the purple form of the exotic *Cerastium vulgatum* in fell-field.

(b) *Schoenus pauciflorus*. Growing in the sun-exposed swamp or bog this species has erect reddish stems, and when dominant forms conspicuous patches. It is also to be found along stream-beds and on wet rocks, where, if in shade, the stems are a deep green and often of a drooping habit. This change may be easily induced by transplanting. But, rarely, in the swamp one meets with plants devoid of the red colouration, growing alongside those of the usual hue. A study of these may show that there are two distinct varieties with constant colour differences, one permanently green, the other able to assume the red colour.

An analogous case is that of *Epilobium melanocaulon*, a plant of debris slopes on the high mountains, where forms with the "typical" blackish stem and dark red leaves may be found growing alongside others with greenish stems and gray-green leaves. There is little doubt that these forms are constant varieties, but a physiological examination of the plants should give valuable results.

(c) *Coprosma brunnea* and *C. acerosa* are two closely allied species differing, among other things, in their colour. The former, an inland plant of dry stony situations, has dark brown leaves and stems, the latter, confined to the coast-line, has yellowish stems and yellow-green leaves. Leaves in the interior of

the bush, in both species, are sometimes quite green. These species illustrate excellently the futility of relying upon herbarium specimens alone in drawing up diagnoses and deciding specific status, dried specimens having much the same colour in each case, and other differences being obscured. A fuller consideration of these forms is to be published elsewhere. It would seem well worth while to grow each in the station of the other.

(d) *Geum parviflorum* usually has green leaves. Specimens gathered by me high up in subalpine herb-field had deep-bronze coloured leaves. These plants cultivated in the lowlands retained their colouration for two seasons, and then gradually assumed the usual green tint. This experience suggests both that epharmonic responses may tend to fix themselves, and that one should not too hastily assume that any particular character is permanent.

H. CONCLUSION

These examples of epharmonic response in plants, together with those recorded in the literature cited, and with others that are accumulating, afford evidence that the taxonomist dealing intensively with species has a most difficult task, and that he must base his decisions regarding critical forms not solely upon herbarium specimens, but must take field and experimental studies into consideration, and bear in mind all the lines of work indicated in the introduction. In this critical taxonomy the phenomena of epharmony take a prominent place. It is the merit of the ecological outlook that it reinforces all branches of botany, freshens their outlook, raises new problems, helps the specialists to get a vista of the science as a whole, and provides a basis for the synthesis of their results. While Hooker's remarks as to the effect of cultivation in changing the form of plants are eminently true, the same responsive changes to environment are found in wild plants, and must be reckoned with. It is evident that so far from the flora of New Zealand being well known we are only at the beginnings. The labours of the past have furnished us with the rough working knowledge on which to build the finished structure.

Du Rietz (17, p. 112) has said, "Eine sehr produktive pflanzensoziologische Schule ist auf Neu-Seeland von L. Cockayne gegründet worden," and, as a humble member of that school I may here be permitted to pay tribute to my friend and master the founder, who has given me unstinted help and critical encouragement since, under his inspiration, I took up the study of botany.

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CHARACTER AND CONDITIONS OF LIFE OF MARINE PHYTOPLANKTON

By BLODWEN LLOYD.

(With five Figures in the Text.)

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I. INTRODUCTORY

Those free-floating unicellular plant organisms grouped collectively as phytoplankton comprise a plant-community as well-marked as those of terrestrial macrophytes. However, although plankton species have been recorded as early as the latter part of the eighteenth century¹, their evaluation as a distinct ecological unit dates from comparatively recent years.

This intensive study has been of later years largely a response to a growing realisation of their importance in the economy of the sea. Here, as on land, the synthesis of the carbohydrates and proteins necessary for animal nutrition is confined to the green plant organisms, which are thus the ultimate source of such organised foods. The whole varied range of animal life is therefore dependent on the two plant-associations found in the sea, namely: (i) the littoral forms, consisting largely of fixed macrophytic algae with also a small proportion of creeping benthic forms, and (ii) the phytoplankton. Now although the former may support a rich fauna locally, their activities are restricted to a comparatively narrow zone fringing the seas, whereas the latter are almost ubiquitous. It follows then that the phytoplankton is the more important unit in considering the organisation of complex food-materials from simple inorganic substances in the sea.

II. CHIEF ORGANISMS OF THE PHYTOPLANKTON

Among the phytoplankton, somatic organisation has not proceeded beyond the stage of the single cell as the complete individual. Within such a "soma-tella" (7), however, we may have a high degree of specialisation for locomo-

¹ *Biddulphia* (*Conferva*) *biddulphiana*, described by Smith, 1762. *Ceratum* (*Cercaria*) *tripos*, described by O. F. Müller, 1781.

tion, flotation, nutrition. Even where a social habit is adopted for better flotation, each cell retains its physiological independence.

Of those species which have succeeded in maintaining an existence in the free-floating habitat, by far the greater number belong to the Diatomaceae or the Dinoflagellata. The former are the more abundant in North temperate and polar seas, particularly in spring and autumn, while the latter abound in warmer regions.

(i) *Diatoms*.

The plankton diatoms exhibit great variety of forms, most of which are variants of the centric type, and are symmetrical either radially or about a median plane. *Coscinodiscus*, one of the simplest and commonest species, is almost drum-like in shape, the numerous discoid chloroplasts lying along the inside of the frustule-wall, and the nucleus being suspended in the centre by a densely granular protoplasmic bridge. This genus consists in all of some 45 species, including some of the largest diatom species (Fig. 1 i).

Several other common species are developmental forms from the *Coscinodiscus*-type; in *Thalassiosira* the frustules are connected by a single mucilaginous thread (Fig. 1 j), and in *Coscinosira* by several, secreted at adjacent valve faces. Other diatoms with circular regular valve view are: *Paralia*, where the frustules are strongly striate and adherent in long filaments; *Bacteriastrum* (Fig. 1 k) and *Corethron*, characterised by a ring of radiate setae around each valve; and *Stephanopyxis*, another filamentous form, bearing a corona of protuberances at the apex of each valve (Fig. 2 c).

Chaetoceras is a very varied genus of over a hundred species. The principal feature is the development on each valve face of a pair of hollow outwardly curved setae. These usually interlock with those of the neighbouring frustule, the terminal setae of a chain often being markedly distinct from the others. There does not, however, appear to be any plasmatic connection between the frustules. *Chaetoceras* is the only important genus which exhibits to a marked degree the social habit, but it seems thus to be well-adapted for flotation in the topmost water layers. Other forms also found floating in the upper surface waters are the numerous species of *Rhizosolenia*. These have an especially prominent girdle view, due to the intercalation between the valves of a number of plates. These may be almost circular, giving the frustule an annular appearance (e.g. *Rhizosolenia stolterfothi*, Fig. 2 a), or they may be rhomboidal in shape with a resulting imbricate effect (*Rh. shrubsolei*, Fig. 1 d and e).

Another numerically important diatom is *Biddulphia* with wide girdle view. The valves are either bilaterally compressed, or 3-4-angled, and possess a more or less pronounced protuberance at each angle. The euplanktonic species have in addition a pair of spines, which are not hollow as those of *Chaetoceras*.

The above are the more prominent diatom members of the phytoplankton, though in addition there are a number of species of the pennate type. These,

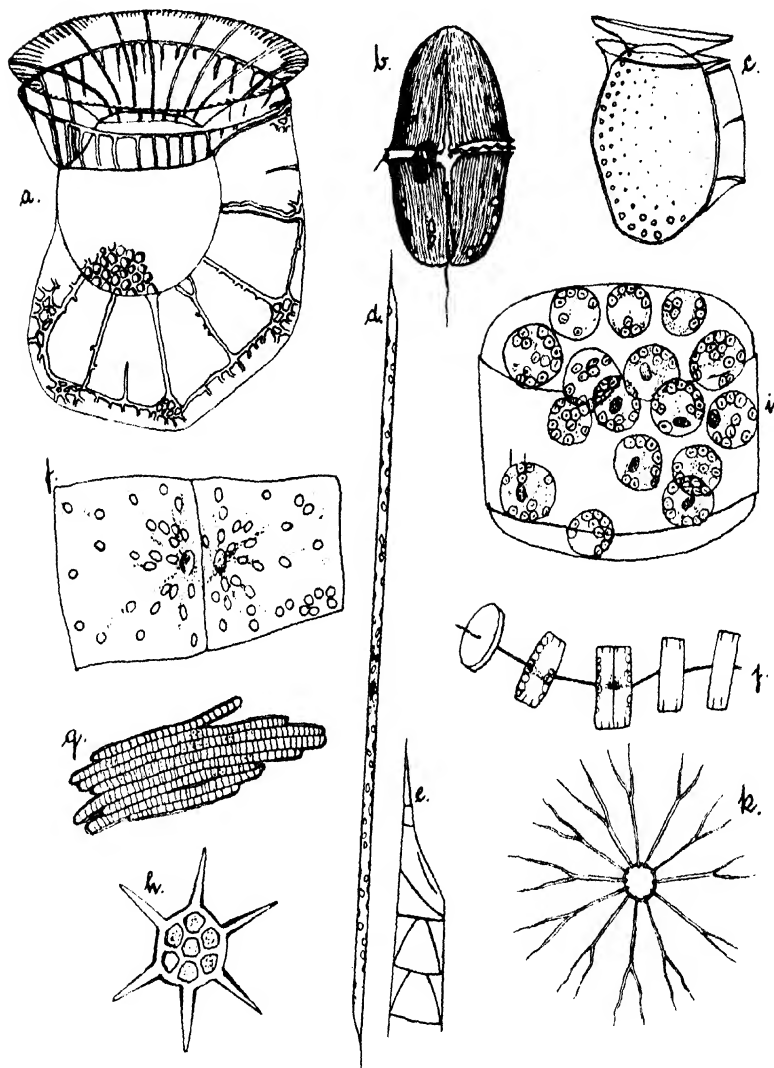


FIG. 1. a. *Ornithocercus steini* Schütt. $\times 400$. Bay of Naples, 17. viii. 25. b. *Gymnodinium diploconus* Schütt. $\times 400$. Bay of Naples, 25. viii. 25. c. *Dinophysis acuta* Ehr. $\times 400$. Plymouth, v. 24. d. *Rhizosolenia shrubsolei* Cleve. e. *Rhizosolenia shrubsolei*. $\times 1000$. f. *Streptothecca thamensis* Shrubsole. $\times 490$. g. *Trichodesmium erythraeum* Ehr. $\times 200$. From Brazil. h. *Distephanus speculum* (Ehr.) Haeckel. $\times 400$. i. *Coscinodiscus concinnus* Wm. Smith. $\times 100$. j. *Thalassiosira gravida* Cleve. $\times 200$. k. *Bacteriastrum varians* Lander. Valve view. $\times 200$.

Camera lucida sketches of specimens taken off the Welsh coasts, except where otherwise stated.

however, although they may be locally abundant in such numbers as to be the dominant form at any given time, do not exhibit such well-marked periodic habit or flotation devices as the true plankton species. Examples of such forms are *Nitzschia closterium*, *N. seriata*, and *Bacillaria paradoxa*. The significance of their occurrence in the plankton is dealt with in Section V.

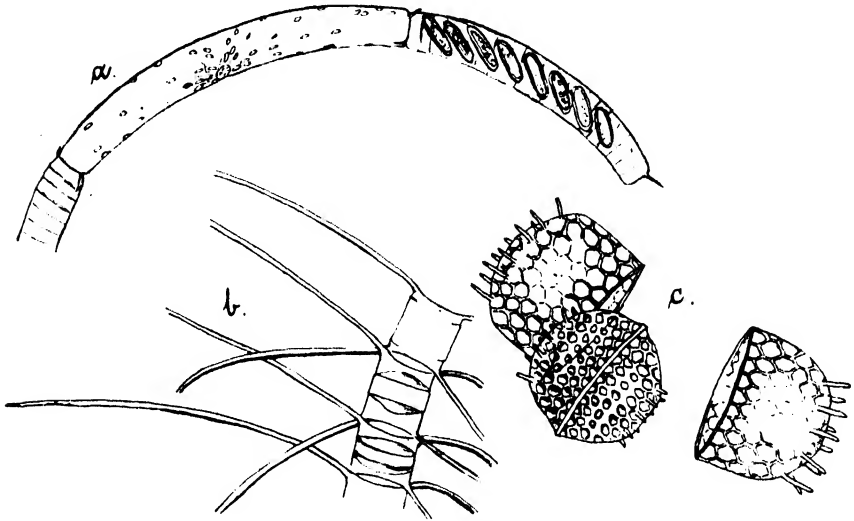


FIG. 2. Resting-spores of plankton-diatoms. All $\times 400$. a. *Rhizosolenia stolterfothi* Perag. Off Aberystwyth. b. *Chaetoceras curvisetum* Cleve. c. *Stephanopyxis turris*. Off Saundersfoot, Pembrokeshire.

(ii) *Dinoflagellata*.

The Dinoflagellata are numerically inferior to the Diatomaceae of the seas, though "in abundance they are second only to the diatoms in the marine plankton, while locally and in midsummer they may far outnumber even these abundant organisms" (7). The particular biologic interest of this group lies in the fact that within the limits of a single genus, for example, *Gymnodinium*, we have methods of nutrition ranging from the purely holophytic to the completely holozoic.

Each of the two subdivisions, namely the Diniferidae with a girdle, and the Adiniferidae without a girdle, contains two parallel groups: (i) those protected by an articulated exoskeleton or theca and (ii) naked forms. Of those species present in the tow-net catches, the thecate forms with a girdle appear to be far more common than the other Dinoflagellata, mainly on account of their greater size, but also because the naked species are easily injured, and are especially susceptible to the changes in their environment consequent upon their capture and transfer to the laboratory.

Of the thecate Diniferidae, the genera *Ceratium* and *Peridinium* are the commonest in North European waters. Here they typically attain a maximal development in the summer months, and both individuals and species are

much more numerous in warmer waters. The presence of the covering theca increases the tendency on the part of the organism to sink; this is compensated for in the less robust and smaller forms by rapid flagellar activity, while in the larger and less mobile, spines and "fins" are often extensively developed, particularly in the tropical and sub-tropical species (Fig. 1 a and c).

Although the thecate forms exhibit great diversity of external structure, it is in the Athecatoideae that we find a greater range of plasmatic specialisation. On the whole, those forms with chromatophores are the more conservative as regards somatic specialisation within the single cell, but in the non-green species we find a range of "organelles" comparable to, and even highly resembling, analogous organs in the Metazoa. Kofoed states that these unarmoured forms reach their optimal development in eupelagic habitats. Certain species, however, are typically neritic, notably those arenicolous forms which colonise intertidal zones in such numbers as to appear to the eye as a discolouration of the sands.

(iii) *Protophyta cetera*.

Apart from the diatoms and the dinoflagellates, there are only a few species which occur in the phytoplankton in any large numbers. Of the Cyanophyceae, *Trichodesmium erythraeum* (Fig. 1 g) may be developed in extraordinary abundance in the warm seas. *Phaeocystis* spp. and *Halosphaera viridis*, brown and green algae respectively which may at any one time become the dominant form, occur in the summer months.

There are also a host of protist forms, some of uncertain systematic position, which occur in small numbers in almost any plankton catch, for example, the silicoflagellate *Distephanus* (Fig. 1 h), or, at a greater distance from land, the calcareous *Coccolithophora*.

III. BIOLOGY OF THE PHYTOPLANKTON

(i) *Periodicity and other Seasonal Changes*.

Variation in external conditions induces variation in the composition of the phytoplankton. Perhaps it would be more accurate to state that with a change in external factors there are concomitant changes in the plankton. The most striking of these is of course the apparent disappearance of some species at certain seasons of the year.

For the diatoms, which in the North temperate zone comprise at most seasons the greater part of the phytoplankton, the periods of maximal development are at about March and September. The absence of most diatoms during the unfavourable period may be accounted for in two ways: (i) that most forms of a given species die out, but leave a few hardy survivors which ensure the continuity of the species, or (ii) that some kind of resting stage is resorted to. The latter is the more reasonable assumption, but at the same time it is

a curious fact that such resting spores are only infrequent, and have not been described for all the known species by any means.

In *Chaetoceras* the highly characteristic resting-spores or "Dauersporen" are formed by the aggregation of the cytoplasm near the girdle-plane and by its subsequent encystment (Fig. 2 b). These spores may bear spinous out-growths on one or both valve faces. The spore of *Stephanopyxis* resembles the parent frustule except for its smaller size and more robust areolation (Fig. 2 c). In *Ditylium* also only one spore is usually formed.

In the genera *Biddulphia* and *Coscinodiscus* the contents divide to form 2-64 nucleated sporules, each with chloroplasts, and a limiting cell-wall (Fig. 1 i). Bergon¹ records motile sporules in the former. A similar phenomenon was once observed by the writer in *Rhizosolenia shrubsolei*, where the cell-contents were divided into eight oval bodies arranged obliquely in the parent frustule (Fig. 2 a).

These spores do not seem to be equipped with any specific adaptation for resisting a rigorous period, so it is reasonable to suppose that they pass the resting period within the parent-cell. Nevertheless, it is remarkable that stages in such spore formation are not more common, particularly at the end of the period of maximal development for any given species. It is stated that these forms sink to their resting level before accomplishing this last act, the sinking being accomplished either by assimilation of the specifically lighter substances such as fats, contained in the cell, or in the bilaterally symmetrical forms by self-orientation upon a different axis, thus offering less resistance to the surrounding medium.

There yet remain to be considered changes in form other than resting stages. The most striking variation is that of size; in certain species, for example *Chaetoceras debile*, summer and winter forms differ so widely that they appear to be distinct species. Other changes in size, however, are not so evidently concurrent with varying external conditions. For instance, the larger, curved forms and smaller straight types of the diatom *Thalassiothrix nitzschoides* were easily distinguished, but no one type appeared to be restricted to any season. Such variations may be due to increased size after auxospore-formation, or possibly to the existence of genetically distinct strains within the limits of the single species.

(ii) *Reproduction.*

Mangin considers plankton diatoms as falling into two groups: (a) those which undergo a period of repose in some form or other, after which period they again begin active cell-division, and (b) dimorphic species with some individuals purely vegetative, and, later, others purely reproductive, only forming endocysts.

It has already been stated that resting stages are found comparatively

¹ P. Bergon. "Nouvelles recherches sur un mode de sporulation observé chez *Biddulphia mobilensis* Bailey." *Travaux de la Station Zoologique d'Arcachon*, 5, 1902.

infrequently; these are formed asexually. Sexual reproduction, as described for many benthic diatoms, has also been described in the plankton-diatom, *Corethron*, by Karsten¹.

Reproduction then in these unicellular forms is mainly a matter of somatic fission, and in both diatoms and dinoflagellates evidences of ordinary cell-division were naturally of frequent occurrence.

With regard to the diatoms of the plankton, the cell-wall is in most cases only slightly silicified, so that successive divisions do not necessarily imply progressive diminution in the size of the frustules, as in the case of the more rigidly silicified phyto-benthon forms. Division of the nucleus is accompanied by infolding of the cytoplasm, the outer layers of which secrete a pair of adjacent valves in the ordinary way. This process is best seen in the larger forms, such as *Biddulphia regia*. Such daughter-cells may remain attached as a short chain, especially when divisions take place in quick succession. Where the adult form normally occurs as a chain the younger cells are often distinguished by the less marked thickening of the walls, and, in the spinous species, by the possession of less robust setae.

In the course of the writer's work on the phytoplankton of the Welsh coasts (8), efforts to obtain stages in nuclear division met with little success, although material was fixed under a variety of conditions and at all hours. No karyokinetic figures were found, and no stages intermediate between the elongated form of the resting nucleus with one or several nucleoli, and the two daughter-nuclei, each with one nucleolus. This may be due to the possibility that division takes place in a plane parallel to the greatest thickness of the cell, and it is difficult to focus high-power lenses through such a bulk of protoplasm. Again, embedding in paraffin and subsequent microtoming gave only distorted forms, due to the tearing of the cell-walls.

Although in the benthic diatoms a simple form of karyokinesis with numerous chromosomes takes place, it is conceivable that division in the more archaic plankton forms is of a much simpler order. Virieux² describes in *Coscinodiscus grani* a karyosomatic type of division; he states that the two nuclei resulting from the fission are each surrounded by a clear perinuclear tract. These zones are connected by a plasmatic bridge which appears to contain chromatinic elements.

In the Dinoflagellata the extra-nuclear cytoplasm is not concerned in cell-division. Nuclear division is karyokinetic, and even in the resting stage the chromatinic thread is distinct; this moniliform structure is characteristic of the dinoflagellates and serves to distinguish encysted stages, which often assume a form very different from the vegetative form.

Cell-division is oblique here. In the thecate forms, as in the diatoms, one part of the exoskeleton goes to each of the daughter-cells, the older half being

¹ Karsten. *Zeitschr. für Bot.* 4, 1912.

² J. Virieux. "Structure et division cellulaire chez *Coscinodiscus grani*." *Bull. biol. de la France et de la Belgique*, 64, 1920.

often distinguishable by the more robust reticulations. Where any such thecate individual fails to divide, there is consequent over-thickening of the theca, with impeding of flagellar mobility. This results in phenomena of rejuvenation, which Kofoed considers as falling into groups: (i) cytecdysis, or shedding of the exoskeleton in pieces of a single or several plates, with ultimate renewal of the whole theca; (ii) cytenuviation, where the whole of the contents is extruded bodily from the theca (7).

(iii) *Nutrition.*

"Morphological distinctions, it has been said, are ultimately physiological ones" (6), and nowhere is this more evident than among the phytoplankton, in which are incorporated the very beginnings of the plant-habit. With the assumption of the chlorophyll-habit, there arises a two-fold necessity, as Church has pointed out (3), for development of a maximum surface for light-absorption, and also for "movements of translation at a rate different from that of the surrounding medium, whether faster or slower." He states further that such fast movement may be accomplished by flagellar activity, but that the nutritive effect may be increased quite as readily by any modification "involving a drag on the surrounding medium." The euplanktonic diatoms, though conceivably descendants of flagellated ancestors, are now non-motile, and are for the most part equipped with spines or protuberances capable of effecting the required "drag." The dinoflagellata, on the other hand, have except in the encysted stage retained the flagellate-habit. Now rapid flagellar activity makes higher demands on the available energy of the organism than the development of mechanical devices such as spines for resisting the tendency to sink. It may therefore be a significant fact that it is some members of this group that have lost the holophytic mode of life—none of the planktonic diatoms, on the other hand, are heterotrophic.

As to the actual food of the diatoms and the autotrophic dinoflagellata, since they are surrounded by their nutritive medium, there is never any problem of insufficiency of water and the commoner salts. At the same time, by the operation of Liebig's Law of the Minimum, any variation in those necessary substances present in minimal quantity will naturally affect the abundance of plankton forms. "The carbonic acid and the mineral salts are present in relatively large amounts, but the proportions of nitrogen compounds, silica and phosphoric acid in the water of the sea are very small. . . . It is probable that the abundance of nitrogen compounds in the sea determines the production" (6). Evidence of this is given by Pearsall (9), who shows that diatom maxima are coincident with, and presumably affected by, spring and autumn river floods, which carry seawards an increased amount of soluble terrestrial compounds, including nitrates and phosphates.

By virtue of their ability to build these simple substances into complex organic compounds, the phytoplankton forms act as the "producers" of food

in the sea. All other non-green living forms, both plants and animals, which utilise these organised substances, are the "consumers."

IV. EXTERNAL CONDITIONS

The constituent species of the phytoplankton exhibit a striking seasonal development, like that of terrestrial plants: the direct causes of this periodicity are equally hypothetical. Herdman (5) ascribes such periodicity in marine plankton organisms to any or all of the three following causes:

- (i) Sequence and periodicity of stages in the life-history of the organisms.
- (ii) Irregularities due to the interaction of the organisms.
- (iii) Periodic changes in the weather, composition of the sea-water, etc.

The two latter are more easily considered than the former, for, "in spite of the incredible amount of investigation that has been lavished on the speciology of this group, much remains to be discovered with regard to the reproduction and life-processes" (6).

The consensus of opinion is that such seasonal changes in the plankton associations are at least a reaction to, if not a direct result of, the stimulus of external conditions, though there is great diversity of thought as to which particular factor or group of factors is mainly responsible. The chief factors are considered briefly below; where any two factors seem to be causally connected, they are considered together.

(i) *Light and Depth.*

Schimper¹ states that the decisive factor in *water is light, while to heat little or no importance attaches*; Schiller² holds that light and probably also the salt-content are the determining factors. At all events, since the "producers" of the sea utilise solar energy as a source of anabolic power, such organisms will tend to dispose themselves both in time and place with regard to the same, such reaction not of necessity being a positive one. "Probably the vernal increase in phytoplankton depends on the rapid increase of the amount of solar energy which accompanies the lengthening days of early spring, especially about the vernal equinox" (5).

If the sunshine curve for Aberystwyth waters be considered (Fig. 3), it will be seen that there is a general but by no means marked agreement with the volume of phytoplankton. Indeed, during the winter months, the volumetric variation seems to follow the temperature curve rather better. This divergence for the winter months is probably directly attributable to the fact that the more intense insolation in the summer months has a greater actinic value to the phytoplankton than the relatively impotent oblique rays towards the winter solstice. The influence of sunshine appears to be due rather to intensity of light than to duration.

Now the efficient plankton organism contrives to maintain itself floating

¹ Schimper. *Pflanzengeographie auf physiologischer Grundlage*, Jena, 1898.

² Schiller. "Vorläufige Ergebnisse der Phytoplankton-Untersuchungen auf den Fahrten S.M.S. *Najade* in der Adria." *Sitzungsab. Kais. Akad. Wiss. Wien*, **122**, 1913. Ref. in this JOURNAL, **2**, 1914, p. 124.

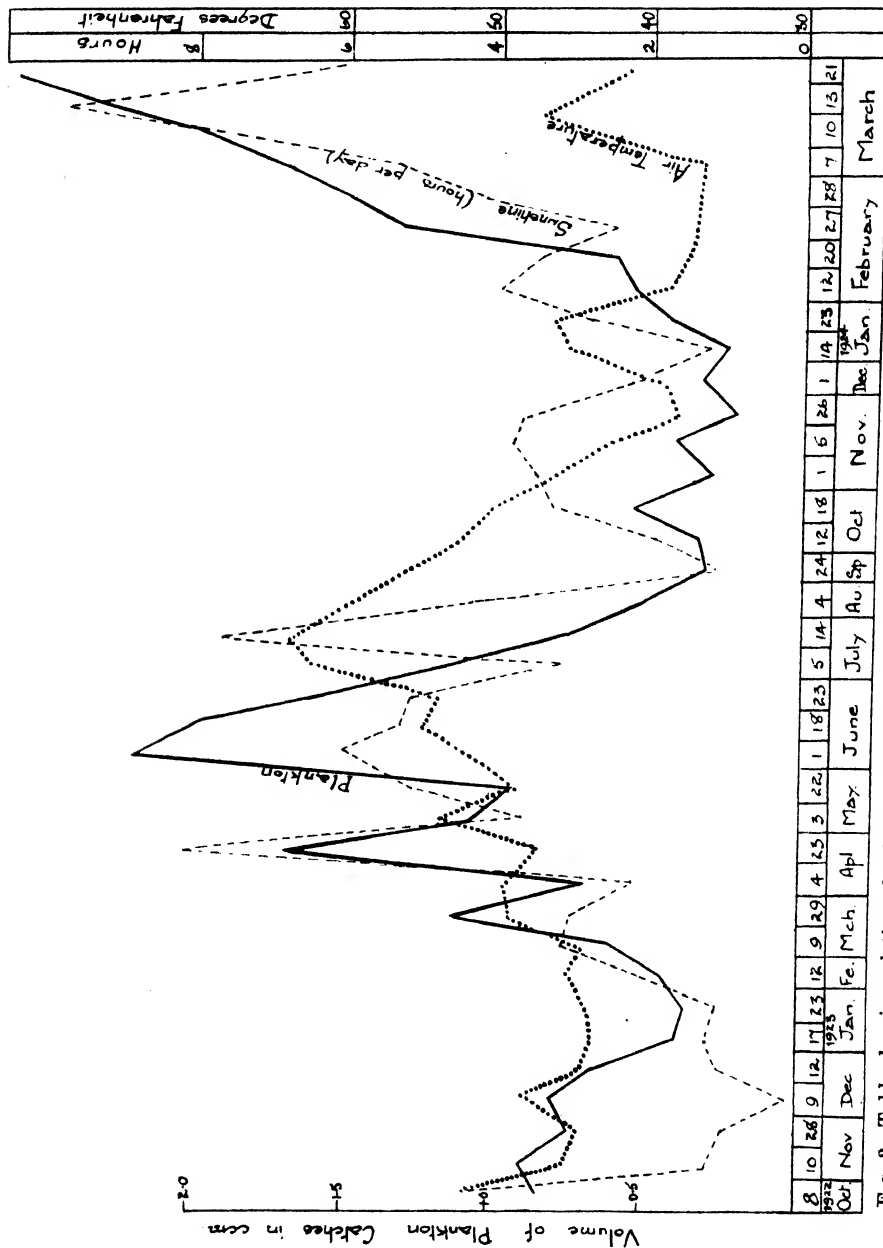


FIG. 3. Table showing relation of volume of plankton to sunshine and temperature. Catches made off Aberystwyth, Cardigan Bay; other data from Meteorological Office Reports.

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at or near the surface, where the sunlight is naturally strongest. The less successful are found at lower and less bright levels, and exhibit a progressive variation in endochrome. Species common in the uppermost layers guard against excessive illumination by the movement of the chromoplasts along the plasmatic strands so as to be mutually protective. Those forms of the top-most water-layers are characterised by the possession of bright yellow-green chromoplasts, usually small and discoid, with a central pyrenoid; *Rhizosolenia* and *Chaetoceras* are the foremost examples of this group. The contrast is the more striking when the two types are compared *en masse*. Viewed in bulk, a surface catch of *Rhizosolenia* and *Chaetoceras* is several shades lighter than a sub-surface haul of *Coscinodiscus* and *Biddulphia*.

Bottom forms are for the most part pennate, and are characterised by the possession of dark yellow or brown chromatophores. These are not truly planktonic, but are often present in catches taken over shallow waters, especially in rough weather.

(ii) *Temperature.*

Temperature appears to affect the spatial distribution of the plankton, in so far as differences of temperature in the sea set up oceanic currents which are largely responsible for the geographic distribution of plankton forms. With regard to the seasonal distribution, however, we must take into account the fact that the phytoplankton rise takes place when the sea is at its coldest in March, with a second rise when at its warmest in September. Obviously then temperature is not a prime factor affecting the periodicity of the phytoplankton. "The predominant assumption in the literature dealing with algal periodicity is that these periodic changes are due chiefly to temperature variations; it makes one suspect that the real underlying causes are factors which normally operate during cold weather, but which may have no causal connection with temperature" (9).

(iii) *Winds, Tides and Currents.*

The indirect influence of winds on plankton distribution by setting up surface-streaming is naturally considerable; local currents and tidal-streaming are largely dependent on these. At the same time, it is debatable as to how far the distribution of plankton is limited by such streams. It has been maintained that these passively floating forms are cast up on the edges of marine currents in much the same way as a river casts up scum and floating objects on its banks; that is to say, that the plankton is disposed in "streaks" or lenticular areas with their long axes parallel to the currents in question.

A second aspect of the effect of tides and winds on the plankton is the mechanical one of increased aeration of the water. It is a well-known fact that flagellated Chlorophyceae tend to develop in enormous numbers in rain-puddles, as, in its passage through the air, the rain dissolves a high proportion of oxygen from the air. Similarly, the beating of the waters into surf-crested

waves, or even the rippling of the surface, makes for the solution of a higher proportion of dissolved oxygen and other atmospheric gases in the sea-water; this induces increased metabolic activity on the part of the contained organisms. In like manner, the waters of rapidly-moving currents tend to have a higher quantity of dissolved gases; "it is well-known that in coastal waters favourite line-fishing localities are where strong tides run through narrow channels over rocks and banks, and these are just the places where of recent years it has been found that plankton is most abundant¹."

(iv) *Salinity and Rainfall.*

These two factors are closely connected, for, although the direct effect of rainfall in lowering the salinity of the sea is negligible for all but the topmost layers, its influence is considerable in its swelling of the volume of the rivers, and hence lowering the salinity for miles off their embouchures. Herdman states that "a heavy fall of rain, sunshine, alternation of night and day, and such phenomena probably have a considerable influence on the vertical distribution of plankton." In practice, tow-nettings made during or after a heavy rain show a drop in volume; this, however, may be due to a purely mechanical cause, namely, the difficulty of tow-netting in a rough sea, or possibly the question resolves itself into a physical one; that is, the sudden lowering of the salinity of the topmost waters would cause the passive plankton forms to sink to lower layers of greater salinity. Apart from this, variation in salinity appears to have no deleterious effect on plankton considered as living organisms; Allen (1) states that, provided that the conditions of light, temperature and mineral foods are favourable, salinity may be varied within very wide limits.

No single factor then appears to control the periodic disappearance of certain phytoplankton species; Johnstone, addressing the British Association in 1923, stated that "the factor influencing actual abundance appears to be a statistical one, a chance association of sub-factors, and not at all any single events, or even a few main events in the sea." Again, this periodicity has been stated to be a purely vital phenomenon entirely independent of external factors: "I therefore class this periodic growth, these . . . cycles which cause volumetric pulses, under the head of internal factor. The element of periodicity in itself does not seem to be consequent upon any known external factor" (Kofoid).

V. EVOLUTION OF THE PLANKTON DIATOM FORM

"The beginnings of botany," writes Church, "are in the sea." In considering the development of living matter from the non-living ionic marine phase, he has presented a scheme of progressive evolution from the specialised ionic "centres of action" in the sea, to the primitive spheroidal protoplasmic unit, and thence to what he designates the "euglenoid phase of flagellar activity."

¹ Herdman, Scott and Lewis. "Intensive Study of the Plankton round the South end of the Isle of Man, Part VI." *Reports of the Lancashire Sea Fisheries Laboratory*, 21, 1912.

The main line of evolution progresses towards, and by way of, the benthic habit; but, in the world of free-floating forms, the euglenoid phase leads, if we except only a few isolated forms, to ultimate divergent specialisation in (a) the dinoflagellata, and (b) the now a-flagellated diatomaceae.

At the present day both these groups are racially impotent, and probably therefore represent termini of evolutionary branches. The phytoplankton organism is a highly specialised but now necessarily static form, for conditions are such that as plankton it is physically impossible for an organism to advance beyond the unicellular stage, and specialisation with the single cell as unit of somatic organisation invariably leads along an evolutionary *cul-de-sac*. In both the diatomaceae, then, and the dinoflagellata, we have groups which have succeeded in maintaining themselves as free-floating organisms since pre-benthic times. For new phyletic developments we must look to those forms which have adopted the fixed habit as opposed to the planktonic.

An attempt is here made to consider the general relationships within the most important phytoplankton phylum in North temperate seas, namely the diatomaceae.

Schütt and others state that the phytoplankton, more especially the diatoms, attains its optimal development in relatively shallow areas not far removed from land. Now the benthic is held to be a post-planktonic stage in racial evolution; in considering the development of the former from the latter, the question therefore arises of the inter-relationship of the phytoplankton with terrestrial factors. As the sea receded, and pristine land masses appeared, moribund plankton forms, it is presumed, acquired a new lease of racial life by adopting the benthic habit; they became either species fixed at the margins of the water, or motile forms creeping along the floor of the shallow coastal seas. The first assumption of the benthic habit, then, would appear to date from, or just before, the first elevation of land.

In considering the geographical distribution of the plankton diatoms, we note the fact, recorded since the days of the *Challenger* Expedition, that they are especially abundant in areas of low salinity with a high nitrate, phosphate and organic content—more especially those seas where large rivers empty themselves. From a consideration of this fact it is therefore suggested that, although these plankton diatom forms may have existed as such beforehand, yet the plankton phase *par excellence* followed *after* terrestrial elevation had taken place, and *after* water erosion had carved out the rivers. Some groups of the phytoplankton therefore may at least be coeval with, if not of later origin than, the primitive benthic protophyte. At all events, the terrestrial factor was undoubtedly a significant one.

In considering the phyletic units of the phytoplankton, it is a significant fact that those forms which compose by far the greater bulk of the tow-net catches throughout the year belong to only four genera, namely, *Rhizosolenia*,

Chaetoceras, *Biddulphia* and *Coscinodiscus*, but that these genera comprise numerous species. If numerical superiority is any measure of success, then these may be held to represent the uppermost limits of evolution among the phytoplankton. For an elucidation of the course of any such evolution one should look, not to these pre-eminent forms, but rather to those static residual genera of only one or perhaps two species, which have apparently had only a moderate success in the plankton phase. Such forms are: *Stephanopyxis turris*, *Lithodesmium undulatum*, *Streptotheca thamensis*, and *Eucampia zoodiacus*. The first-named has a valval corona of protuberances through which protoplasmic connections are stated to pass into the neighbouring frustule; in the second case, the frustules are united in long filaments bearing a superficial resemblance to a filamentous brown alga; the last two examples possess a rudimentary central nodule—all these being tentative developments towards a somatic organisation of increasing complexity. Whether these are instances of parallel development, or whether they indicate the protodiatom forms from which the plankton diatom proper, the phytobenthon and epiphytic diatoms respectively have diverged, is naturally not determinable from morphological evidence alone. At all events, there are two distinct phyletic tracks, with also a third less marked, for the phytoplankton form as seen in the sea to-day.

(i) *Typical Diatom Forms—widely distributed abundant species.*

The typical plankton forms comprise those highly successful widely distributed genera of many species which are very variable in form and which correspond to such "critical" genera among land plants as *Rubus* or *Hieracium*. To this class belong the four genera enumerated previously, namely, *Rhizosolenia*, *Chaetoceras*, *Biddulphia* and *Coscinodiscus*.

Among aquatic phanerogams, the ease with which the necessary foods are obtainable results in morphological degeneracy; in the phytoplankton, however, this relative abundance of water and nutrient salts is more than counterbalanced by the physical necessity for adequate flotation-equipment. Those forms then found free-floating in large numbers are those which have succeeded in maintaining a suitable plankton-soma—usually as the unicellular individual.

Both *Rhizosolenia* and *Chaetoceras* are genera with wide specific variation, the former consisting of about 60 species and the latter of well over a hundred. In each the elongated form is assumed; in *Rhizosolenia* this is accomplished by the intercalation of numerous plates between the valves, resulting in an enormously lengthened girdle view. In *Chaetoceras*, although each frustule is as broad as long, the individuals hang together by spinous outgrowths, giving here again the slender and long floating form. The social habit is then the rule in the latter case, whereas it is the exception in the former. Each genus has one species which has gone along a specialised line in the evolution of the

plankton-soma, and has adopted the "coiled" habit. In *Chaetoceras sociale* the frustules are grouped in an open circle, the incurved setae giving to the colony a disc-form strengthened by the ribs directed radially towards the centre, and also by the production of mucilage. In *Rh. stollerfothi* the frustules are curved, and the chains of cells thus overlie one another in a loose spiral (Fig. 2 a). These two species show development parallel with the coiled limnetic habit adopted by *Mougeotia* and other Conjugatae, when found free-floating in freshwater lakes.

Both *Rhizosolenia* and *Chaetoceras* are pre-eminent in numbers of species and individuals; at the same time, they are found in greatest numbers at the surface. These two genera then appear to be the optimum expression of the plankton habit among the diatoms of the sea.

At a somewhat lower water-level are *Biddulphia* and *Coscinodiscus*, forms moderately bulky in proportion to the surface area, and hence less mobile. They are less mobile in the evolutionary sense also, for their component species are much more static and more exactly delimited than the above-named. It follows therefore that they are of a lower grade in order of plankton efficiency; moribund species then, to ensure the continuity of their racial life, must perforce adopt a non-planktonic mode of life—and this is what appears to have happened. No species of *Rhizosolenia* or *Chaetoceras* occur among the epiphytic littoral forms, but several species of *Biddulphia* and many of the *Coscinodiscus*-type are known.

Dealing first with *Biddulphia*, we find here a genus whose component species range in habit from the euplanktonic through varying degrees to the truly epiphytic. *B. mobiliensis* and *B. granulata* are true plankton species (Fig. 4 a, b, f), as witnessed by their dorsiventral compression and valval spines and protuberances. All three species are found in the open sea. A morphologically intermediate planktonic species with absent or inconspicuous spines, abortive protuberances and ventricose valve view is *B. rhombus* (Fig. 4 c), which is especially common during the early months of the year within half-a-mile of the sea-shore. It is rarely found at any considerable distance from land, and presents a form midway between such as the three first-named species, and the characteristic coast-line species of planktonic Biddulphias, which are angular in valve view, as, for example, *B. favus* (Fig. 4 d). A closely related free-floating littoral form is the rather rarer *B. alternans* (Fig. 4 e). The resulting difference in habit is well shown by the greater silicification and more robust areolation of the former, though both species have apparently sprung from a common stock. The ultimate stage in this series is represented by the shore-type *B. vesiculosa*, which, although an occasional constituent of the littoral hemiplankton, occurs normally as zig-zag epiphytic filaments (Fig. 4 g).

The genus *Coscinodiscus* does not show so complete a series of intergrades as *Biddulphia*. They are all of the drum-like form, one of the most conspicuous

being the large species, *C. concinnus* (Fig. 1 i). Although there is little variation within this genus, a large proportion of the diatoms of the various fossil deposits are developmental forms from the *Coscinodiscus*-type, so that we have here survivors of a group that has attained considerable numbers in the past. Many of these are now extinct; this race is now represented in the plankton by certain well-defined species which have succeeded in maintaining the balance of racial efficiency in their favour.

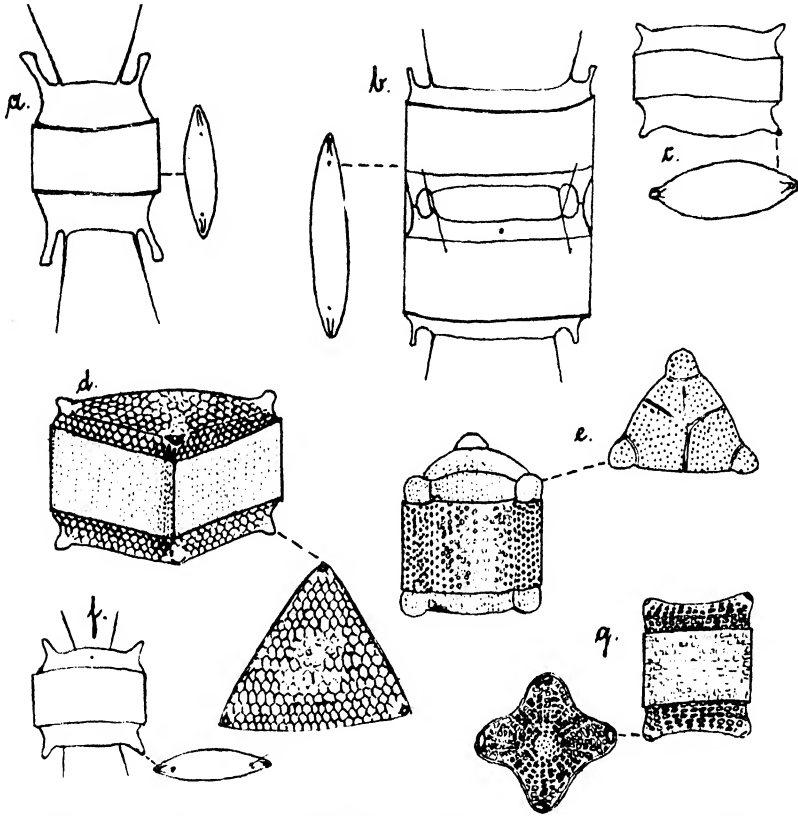


FIG. 4. Progressive variation in *Biddulphia* according to habitat. All except (b) $\times 200$. N. European species. a. *B. mobiliensis* (Bailey) Grün. b. *B. mobiliensis* (Bailey) Grün. forma *regia* Schutze $\times 100$. c. *B. rhombus* (Ehr.) Wm. Smith. d. *B. favus* (van Heurck). e. *B. alternans* (Bailey) van Heurck. f. *B. granulata* Roper. g. *B. vesiculosa* Boyer.

(ii) *Residual Plankton Forms*—of less abundance.

Turning to those isolated genera I have termed residual plankton forms, it will be noticed that the distinction from the former group is mainly one of numerical inferiority. It is from these failed and failing groups that, given sufficient impetus, new modes of life might be tentatively adopted. It has already been noted that most of the marine plankton forms are centric. Two species, *Streptotheca* and *Eucampia*, have a rudimentary central nodule. The

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central nodule, important in the structure of the motile diatoms, is here apparently functionless, since they do not appear to move. Both these forms are distinct genera of limited distribution in time and place.

Two other genera, each of one species and with uncertain affinities, are *Bellerochea* and *Climacodium*. Possibly then this isolated and biologically insignificant group may be a surviving stage of the experimental forms of the early plankton phases.

(iii) *Reversionary Plankton Forms.*

The third group comprises all those forms which exhibit evidences of reversion to a planktonic from a previous benthic habit. I exclude of course such fortuitously free-floating forms as *Navicula* spp. or *Pleurosigma* spp., swirled from the bottom into the upper waters by external factors, and propose to consider only those forms which are purposively planktonic. These are all of the pennate type, and, having lost whatever planktonic adaptations they possessed in the pre-benthic state, must needs acquire a new flotation mechanism—since they cannot regain lost adaptations by retracing their evolutionary path.

This class is a well-defined group in the sea. They differ from the euplankton by the fact that they only rarely attain any great numbers—*Asterionella*, *Nitzschia seriata* and *N. closterium* are the principal ones—and that they do not show to any marked degree the bi-modal periodic curve characteristic of the phytoplankton proper. They are, in fact, comparable in many ways to the diatoms of the freshwater plankton. In both cases the greater number are pennate; in fact, the following representative list (10) shows both groups to comprise identical genera:

MARINE.	FRESHWATER.
<i>Thalassiothrix</i> (<i>Synedra</i>)	<i>Synedra</i>
<i>Asterionella</i>	<i>Asterionella</i>
<i>Bacillaria</i>	—
<i>Fragillaria</i>	<i>Fragillaria</i>
<i>Nitzschia</i>	<i>Nitzschia</i>
—	<i>Tabellaria</i>

The two first-named genera, *Thalassiothrix* and *Asterionella*, are both characterised by the union of their rod-shaped frustules into a star-shaped or occasionally zig-zag colony. By far the greater number of species of *Synedra* are epiphytic, but a few species have returned to a free-floating habit, firstly as a free-floating littoral zig-zag form, and later as a pelagic star form, which Wesenberg-Lund considers an adaptation of the former.

In contrast to these reversions from the sessile benthic to the planktonic, we have in *Bacillaria paradoxa* a retrogression from the motile benthic habit. Instead of the development of a special flotation form as in the case of

Thalassiothrix, this species has retained its power of motion to ensure a differential rate of movement in the surface-waters. As the frustules glide backwards and forwards past one another, they come into contact with different parts of the surrounding medium for nutrition, while at the same time the narrow bacillar frustules, disposed horizontally when extended, offer as much resistance as, for example, a *Rhizosolenia*, against over-rapid sinking. A similar flotation mechanism is observed in *Nitzschia seriata*, where the frustules can by gliding in the same way arrange themselves end to end in elongated series.

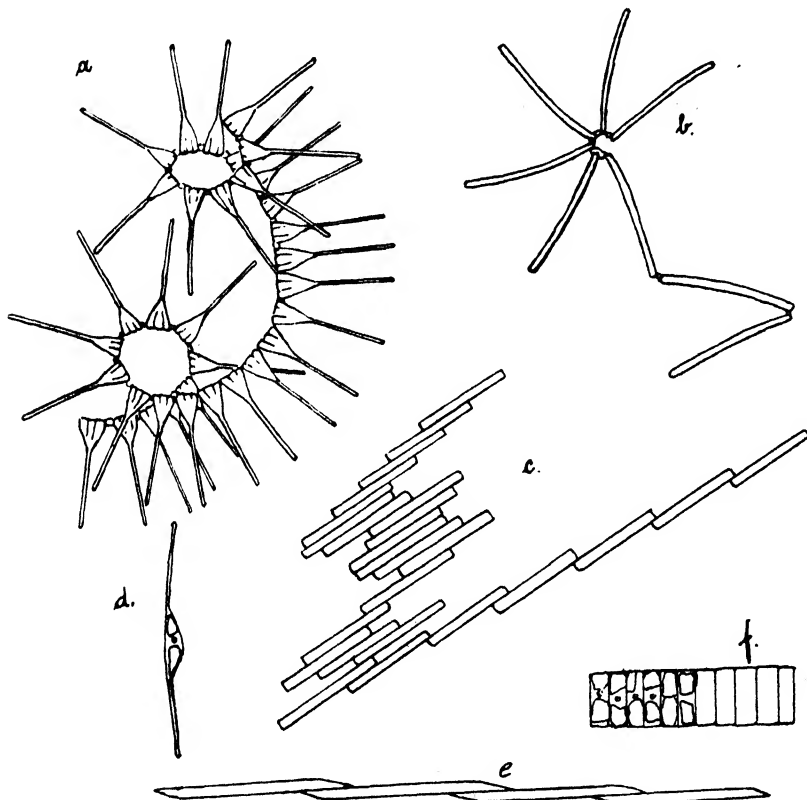


FIG. 5. Retrograde plankton diatoms. All $\times 200$. a. *Asterionella japonica* Cleve. b. *Thalassiothrix nitzschioides* Grun. c. *Bacillaria paradoxa* Gmel. d. *Nitzschia closterium* Wm. Smith. e. *Nitzschia seriata* Cleve. f. *Fragillaria oceanica* Cleve.

The case of *Nitzschia closterium* is even more interesting. Two distinct forms are recorded. Both types are abundant in cultures; the larger is motile, but the smaller non-motile. Furthermore, in vertical plankton hauls containing a bigger proportion of bottom forms than horizontal hauls, the latter variation of *N. closterium* is more frequent. Lebour¹ states that this is an adult form

¹ Lebour, M. V. "The Microplankton of Plymouth Sound." *Journ. Marine Biological Association*, 1917.

of the smaller one. Here then we appear to have in the plant world an organism with two stages in its life-history, a planktonic followed by a benthic stage, this being analogous with those marine animals such as *Balanus*, whose larval stages are free-floating, but whose adult forms are benthic.

The above is an attempt to indicate that the term plankton, as far as the diatoms at least are concerned, comprises a polyphyletic assembly of species with different racial history but similar habit; or, as Church has said, "Plankton is more physiological than morphological."

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THE WATER-RETAINING POWER OF THE SOIL

By H. C. HANSEN.

(From the Plant Physiological Laboratory of the University of Copenhagen.)

(With three Figures in the Text.)

By the water capacity of a soil is understood the quantity of water which a given soil is capable of retaining. It is expressed as a percentage of the volume of that soil.

There is considerable variation in the water capacity, according to the size of the soil particles. The more finely divided the soil, the higher its water capacity, as will be seen from the following table (from *Boden und Klima auf kleinstem Raum*, by G. Kraus):

Table I.

Percentage of soil particles larger than 0.5 mm.	Water capacity
89.7	9.19
89.5	10.5
82.72	14.51
58.19	18.6
56.6	19.34
31.0	29.4
17.02	30.26
0 (washed soil)	28.0-52.0

Of the water thus retained by the soil, a portion remains adhering to the soil particles as a thin layer held by adsorption, while the rest collects in small hollows and crevices, where it is retained by capillarity. Gradually, as the amount of water in the soil becomes less—as a result of evaporation, for instance—the water held by capillarity will be the first to disappear, then the water retained by adsorption. While the retaining power of the capillarity is only slight the adsorbed water is held back with rather considerable force.

For a plant to be capable of drawing water from the soil, the force with which it sucks up the water must be stronger than that with which the soil holds the water back; and the results of numerous experiments go to show that plants are generally capable of absorbing the water that is held by capillarity, but not—or, at most, only partly—the water held by adsorption. If, now, a plant of some kind is grown in the soil, without any more water being supplied to the latter, the quantity of water which the soil contained at the beginning of the experiment will gradually be reduced, until the plant finally wilts, because the absorptive force of the roots can no longer overcome

the water-holding power of the soil, though there will still, at that moment, be a certain amount of water left in the soil.

If specimens of the same kind of plant are grown in different soils, it is safe to suppose that the water-retaining power of these soils will be the same at the moment when the plants wilt. The water content, on the other hand, at the moment of wilting, will be different in the different soils. This is made evident by the results of an experiment, made by Sachs, in 1859, with tobacco plants:

Table II.

Soil	Original water content in 100 grams dry weight	Water content at the moment of plant wilting	
		grams	% max. content
Sand and humus	46.0	12.3	27
Clay	52.1	8.0	15
Coarse quartz sand	20.8	1.5	7

The result of this experiment shows the water-retaining power of the quartz sand to be rather feeble as compared with that of the clay soil or of sand mixed with humus.

For these reasons, a simple determination of the water content of the soil does not furnish any basis for a true estimation of the amount of water actually at the disposal of the plants. To determine this, it will be necessary to proceed differently; namely, by trying to determine the water-retaining power of the different soils with various contained water percentages. The present paper is an attempt in that direction.

As an introduction, let us review, very briefly, some of the earlier investigations made for the purpose of determining the water-retaining power of the soil. The methods employed to that end have been partly physical, partly biological.

1. *Physical methods.* **Livingston** (1906) places in the soil to be studied an artificial root hair, in the form of a semipermeable "Pfeffer's cell," filled with a 1.5 to 2 molecular solution of cane sugar, and then determines whether this osmometer absorbs the water from the soil, or whether a movement in the opposite direction takes place. As the result of a couple of experiments it was found that the absorption, by the osmometer, did not begin until the water content of the soil was brought up to 20 or 25 per cent. **König, Hasenbäumer** and **Grossmann** (1908) placed the soil to be examined in a "Pfeffer's cell," poured water over it, and measured the osmotic pressure after the cell had been sunk in water. The figure obtained thus indicates the degree of osmotic pressure exerted by the soil water (though in a diluted state). **Shull** (1916) determined the water content of *Xanthium* seeds that had lain in the soil, and from the results thus obtained he was again able to calculate the degree of the osmotic pressure by which the water was retained in the soil, by comparing them with measurements previously made of the water contents of other *Xanthium* seeds that had been lying in solutions of various concen-

tration and of known osmotic strength. As a means of determining the water-retaining power of the soil, **Livingston** and **Koketsu** (1920) measured the amount of water absorbed within a given time by a hollow, cone-shaped cylinder of porous porcelain. Other investigators, like **Van Bemmelen** (1910) and **Odén** (1919), determined the vapour pressure in humus by placing the dried sample of soil in a desiccator over a sulphuric acid solution of known concentration and vapour pressure. When equilibrium has been attained, the water content of the sample is determined, and it is then placed in another desiccator over a slightly more concentrated solution of sulphuric acid. When the equilibrium is once more established, the water content of the sample is determined a second time; and by continuing in this manner and noting, one after another, the values thus obtained, a curve will result, showing the dependence of the vapour pressure on the water content of the humus. **Thomas** (1921) estimates the water pressure in three different soils. His method consists in passing a known volume of air through the soil, collecting and weighing the vapour. He finds that the vapour pressure is a linear function of the reciprocal of the moisture content over a wide range.

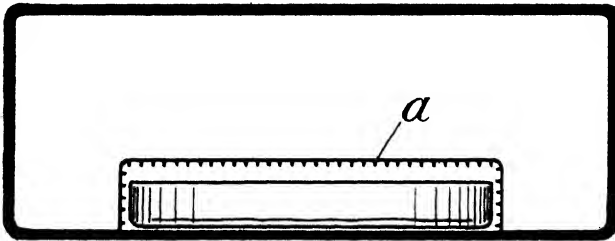


FIG. 1.

II. *Biological methods.* **Briggs** and **Shantz** (1912) determined the wilting coefficient for various soils by the "wax-seal method," which is a modification of the method formerly employed by **Sachs**. They find this coefficient to be about the same for a number of different plants, and note that it varies considerably with the character of the soil. **Ursprung** and **Blum** (1921) find the water-holding power of a soil by determining the absorptive power of a root that has grown in it, because these two quantities must be supposed to be equal. The absorptive power of the root is measured by determining the volume of an epidermis cell in its natural state and then measuring the concentration of the cane sugar solution which does not alter the volume of that cell. The water-retaining power of the soil will then be equal to the osmotic pressure of the cane sugar solution.

The method which I have used for measuring the water-retaining power of the soil consists in determining the strength of the sugar solution which has the same vapour pressure as the soil sample under investigation.

The procedure is as follows: in a glass box, $16 \times 6 \times 11$ cm., with a loose glass lid, a piece of nickel-wire netting (a in Fig. 1) 9.5 cm. high by 15.5 cm.

long, and having 2.5 cm. of this length, at each end, bent over at right angles, is placed in such a manner that the bent-over edges rest against the side of the box, forming a small cage, as shown in Fig. 1. The glass box is thus divided into two compartments of unequal size. The soil to be investigated is placed in the larger of these, whereupon the lid is sealed on air-tight by means of vaseline, and the closed box placed in another, larger box lined with cotton

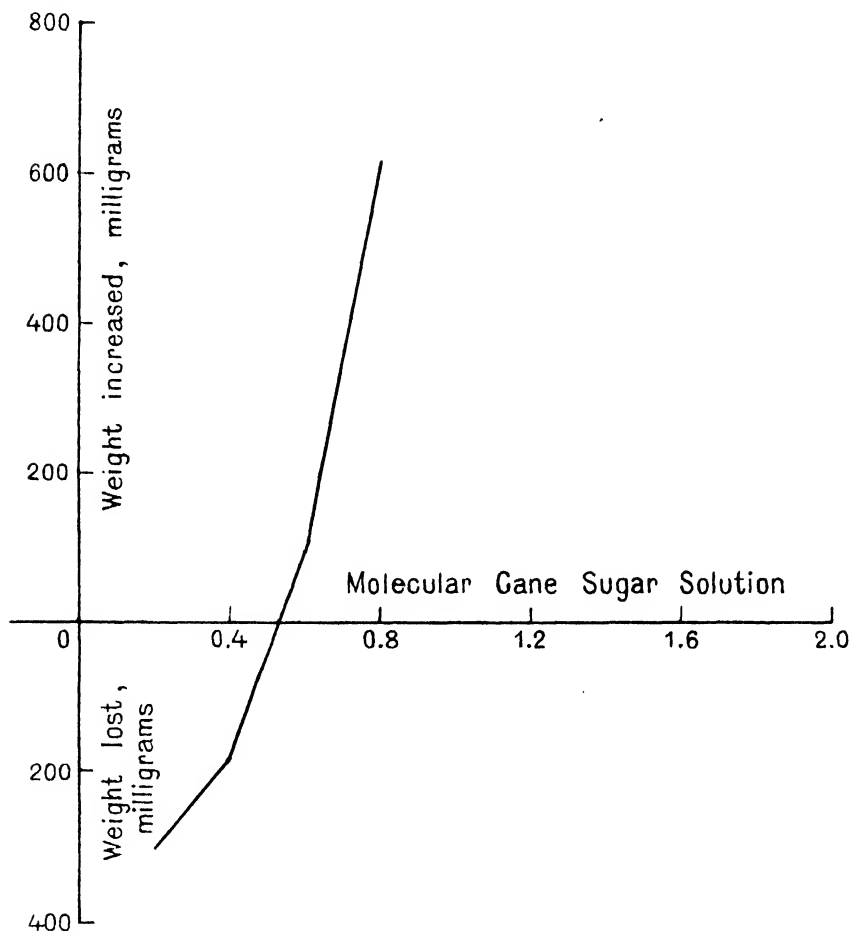


FIG. 2.

wadding, for 24 hours. After that time the glass box is taken out and opened, and in the smaller compartment is placed the bottom part of a Petri dish, 10×1 cm., on the inside of which has been laid a paper filter saturated with a cane sugar solution of a previously determined strength. The lid is then sealed on again with vaseline, and the glass box put back in the wadding-lined receptacle for another 24 hours. After that time the box is opened once more, the Petri dish is taken out, and the lid is put on again. The Petri dish with

the filter is now weighed, and if a similar weighing has been made before the test was begun, it can be ascertained whether the sugar solution has absorbed or given off water; or, in other words, whether the vapour pressure of the sugar solution has been greater or less than the vapour pressure in the soil investigated. If, now, we extend the experiment to comprise—instead of only one glass box, as here described—four or five boxes, all containing the same kind of soil, but with the sugar solution in a different degree of concentration for each of the filters, we shall find, provided these concentrations have been suitably chosen, that the Petri dishes containing the weaker solutions have lost in weight, while those containing the stronger concentrations have become heavier; and by these means it will thus become possible to determine exactly what sugar concentration has the same vapour pressure as the soil under investigation. The easiest way of arriving at this determination is to make it graphically, by plotting the rate of change—that is, the loss, or the increase, in weight—corresponding with the different concentrations, on squared paper, and constructing a curve connecting these various points. The point at which this curve intersects the axis of the abscissae will then mark the degree of concentration of the sugar solution with which the soil sample is in equilibrium.

By thus examining a number of samples, all from the same soil but of different water content, we get, in this manner, an expression for the relation of water-retaining power to water content, in the soil type examined.

Variations in temperature are the chief sources of error in connection with these investigations. If, namely, the soil sample and the sugar solution in the Petri dish are of different temperatures, an over-distillation of water may take place, even if the vapour pressure should be the same in both. Every precaution must therefore be taken to avoid the occurrence of any such variations, and this is done by isolating the glass box as carefully as possible in the cotton-lined outer box, as described.

In order to test the correctness of the method, there were placed in the larger compartment of the glass box strips of paper saturated with an equimolecular potassium nitrate solution, and in the Petri dishes potassium nitrate solutions having a concentration of, respectively, 0.5, 1.0 and 1.5 gm. molecules. The result is shown in Table III.

Table III.

	0.5 mol.	1.0 mol.	1.5 mol.
Experiment I	- 0.08	—	+ 0.065
Experiment II	- 0.07	0.0	+ 0.06

The experiment shows that it is possible to measure more or less approximately the osmotic pressure of a given solution.

By this method I have investigated the reciprocal relation between the water-retaining forces, together with the water content of five different types of soil.

Experiment I. In this series of tests a *pure quartz sand* with a water capacity of 14 per cent. was used. The result of the experiment is given in Table IV:

Table IV.

Water content (%)	4.4	1.84	1.09	0.56	0.21
Mol. cane sugar solution	0	0.42	0.51	0.91	1.82
Osmotic pressure in atmospheres	0	11	14	28	90

Experiment II. The soil used in these tests was *sand mixed with clay*. The sample was entirely free from humus, and on being washed was found to contain 62 per cent. of sand, with a water capacity of 27 per cent.

Table V.

Water content (%)	10.74	7.18	4.81	4.28	3.25	3.15	2.17
Mol. cane sugar solution	0.06	0.18	0.67	0.86	1.35	1.53	1.84
Osmotic pressure in atmospheres	1.5	4	19	26	51	63	92

Experiment III. These tests were made with *garden soil* containing 62 per cent. of sand and 5.25 per cent. of humus. The water capacity was 24 per cent.

Table VI.

Water content (%)	19.35	12.39	9.49	8.66	7.04	6.18	5.67	5.06	4.54
Mol. cane sugar solution	0.1	0.2	0.25	0.3	0.74	0.96	1.24	1.58	1.93
Osmotic pressure in atmospheres	2	5	6	7.5	21	30	45	67.5	100

Experiment IV was made with *pure clay* (modelling clay).

Table VII.

Water content (%)	29.68	23.84	20.47	17.32	13.83	12.1	9.92
Mol. cane sugar solution	0.02	0.06	0.24	0.34	0.51	1.21	1.91
Osmotic pressure in atmospheres	0.5	1.5	6	8.5	14	43	98

Experiment V. In this experiment the soil was *beech mould*. The water capacity was 61 per cent.

Table VIII.

Water content (%)	36.45	29.32	24.0	23.47	19.0	15.83
Mol. cane sugar solution	0.24	0.38	0.44	0.5	0.74	1.7
Osmotic pressure in atmospheres	6	10	12	13.5	21	83

The results of these experiments are represented graphically in the following curves, in which the abscissae denote the water content of the soil type in question, while the ordinates denote the cane sugar solution, or the osmotic pressure corresponding to the various concentrations.

As we might expect from the results of **Sachs'** experiments, the water-retaining power of the sand is extremely slight; only with a water content of 1 per cent. does it reach a strength equal to the osmotic force in a 0.5 molecular cane sugar solution, which corresponds to a pressure of 13 or 14 atmospheres. If we suppose the osmotic pressure at the beginning of plasmol-

lysis in the roots to be about 10 atmospheres, then the intake power also should consequently run no higher than to this value as a maximum; which is equivalent to saying that the absorption of water by the roots ceases when the water content of the soil has sunk to 2 per cent.—a proposition which agrees fairly well with the findings of **Sachs**, that tobacco plants wilted when the water content was 1.5 per cent.

A comparison of the curve for the pure quartz sand with the one for the sand mixed with clay shows that the clay content plays a great rôle as regards the water-retaining power, the latter rising, owing to the presence of the clay, to as much as 13 or 14 atmospheres when the soil contains 5.5 per cent. of water. With a lesser content of water the retaining power of the sand and clay mixture rises somewhat less rapidly than in the pure sand.

The soil which forms the subject of experiment III differs from the one used in experiment II chiefly by its content of humus, and it is noticed that this admixture tends to increase the water-retaining power, which here, for a water content of 8 per cent., reaches between 13 and 14 atmospheres.

It is in pure clay and pure humus that the water-holding power is greatest. In beech mould, as shown by experiment V, it is as high as 13 or 14 atmospheres with a water content of 23 or 24 per cent. As a curious feature it should be noted that with decreasing water content the increase in water-retaining power is much slower here than in the first three experiments.

By this method it is possible, then, to determine more or less approximately

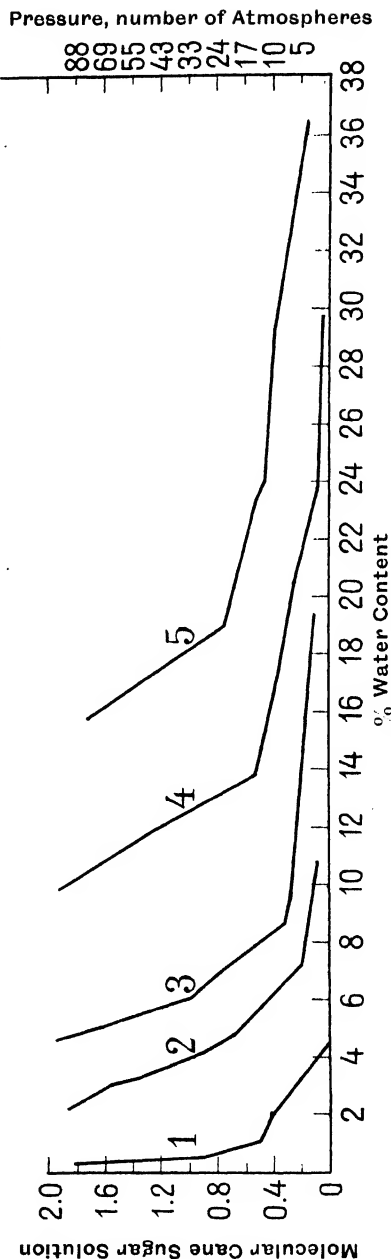


FIG. 3. Curves showing the water-retaining power in different soils: (1) pure quartz sand; (2) sand mixed with clay; (3) garden soil; (4) modelling clay; (5) beech mould.

the vapour pressure in any given soil, and thus the water-retaining power of that soil. It next becomes a question of examining what importance the degree of that power has for the absorption of water through the root system.

For a root to be able to absorb water from a given soil it is necessary that the force with which the absorbing cells of that root suck up the water should be greater than the force by which the water is held back in the soil. The absorptive power of the cell is, in its turn, determined by the strength of the osmotic pressure, less the strength of the sap tension, by which is understood that portion of the osmotic pressure which is exerted on the wall of the cell. The absorptive power can thus vary from zero up to the value of the osmotic pressure exerted under conditions of commencing plasmolysis. As a result of this absorption by the cells the water content in that part of the soil which is in immediate contact with the surface of the root is reduced to a quantity so small that the force by which the water is retained in the soil is equal, or only slightly inferior, to the force with which it is absorbed by the plant. In those parts of the soil which are farther away from the surface of the root, the quantity of water will be greater, and this difference in water content between the different regions of the soil, due to the absorption from the root, will therefore result in a movement of water from the more distant, moister regions toward the surface of the root. It is this movement of the water in the soil which enables the plant to continue its absorption of water. Any increase in the absorptive power of the cell will cause the amount of water in the part of the soil in immediate contact with the root surface to become still further reduced, and the difference in water content between the different parts, which causes the water movement, will thus be all the greater.

The fact that **Fitting** has ascertained the osmotic pressure in a number of desert plants to be relatively high, makes it of interest to examine in what types of soil an increase of the osmotic pressure may possibly have a bearing on the degree of absorption. A look at the curves will show that an increase of the osmotic pressure will not be of any material significance in the case of plants growing in sandy soils, because even with a low osmotic pressure these plants will be able to absorb practically all the water in the soil. In soils containing a great deal of humus or clay, or of both these substances together, and in which the water is, consequently, retained with rather considerable force, an increase in the osmotic pressure may, on the other hand, help to increase the amount of water on which the plants can draw. It is therefore of interest to see that the abnormally high osmotic pressures recorded by **Fitting** were found by him in plants that grew in rock- or desert-crevices filled with clay, while the osmotic pressure of the same plants, when they are grown in sand, is considerably less.

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OBSERVATIONS ON A LUMBERED AREA IN SURREY FROM 1917 TO 1925

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(*With eight Figures in the Text.*)

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INTRODUCTION

During the war a considerable area of forest on the Bagshot Sands in the neighbourhood of Virginia Water was felled by Canadian lumbermen. The land was not immediately replanted and as it lay conveniently near the Royal Holloway College Botanical Laboratory, continuous observations were made to record the natural changes of vegetation over the exposed area (Fig. 1).

A plot of land was chosen for detailed study, about an acre and a half in area, sloping slightly to the south-west. It had been pure pine forest, but outside it, in its near neighbourhood, there stood a few birches among other trees, and this fact explains in part the plant succession that followed.

Observations were continued until January 1925, when the forest authorities of Windsor Great Park cleared the area and replanted it with *Pinus sylvestris*.

HISTORICAL ACCOUNT

THE AREA AT THE OUTSET OF THE INVESTIGATION IN 1917.

The Canadian lumbermen had been at work from June to October 1916 and in November of the next year observations began. At this time there was very little vegetation, the uneven surface of the soil being broken only by numerous tree stumps and certain charred patches, nineteen in number, where the lumbermen had made their large bonfires. The surface of the soil was covered with loose pine needles, below which, to a depth of from 1 to 5 inches,

¹ The work described in this paper was organised and written up by M. Benson (1917-22) and E. M. Blackwell (1922-25) with the help of notes and maps made by D. M. Adkins (Mrs Burrows), 1915-20 and M. I. Thomas, 1921-25, Royal Holloway College, University of London.

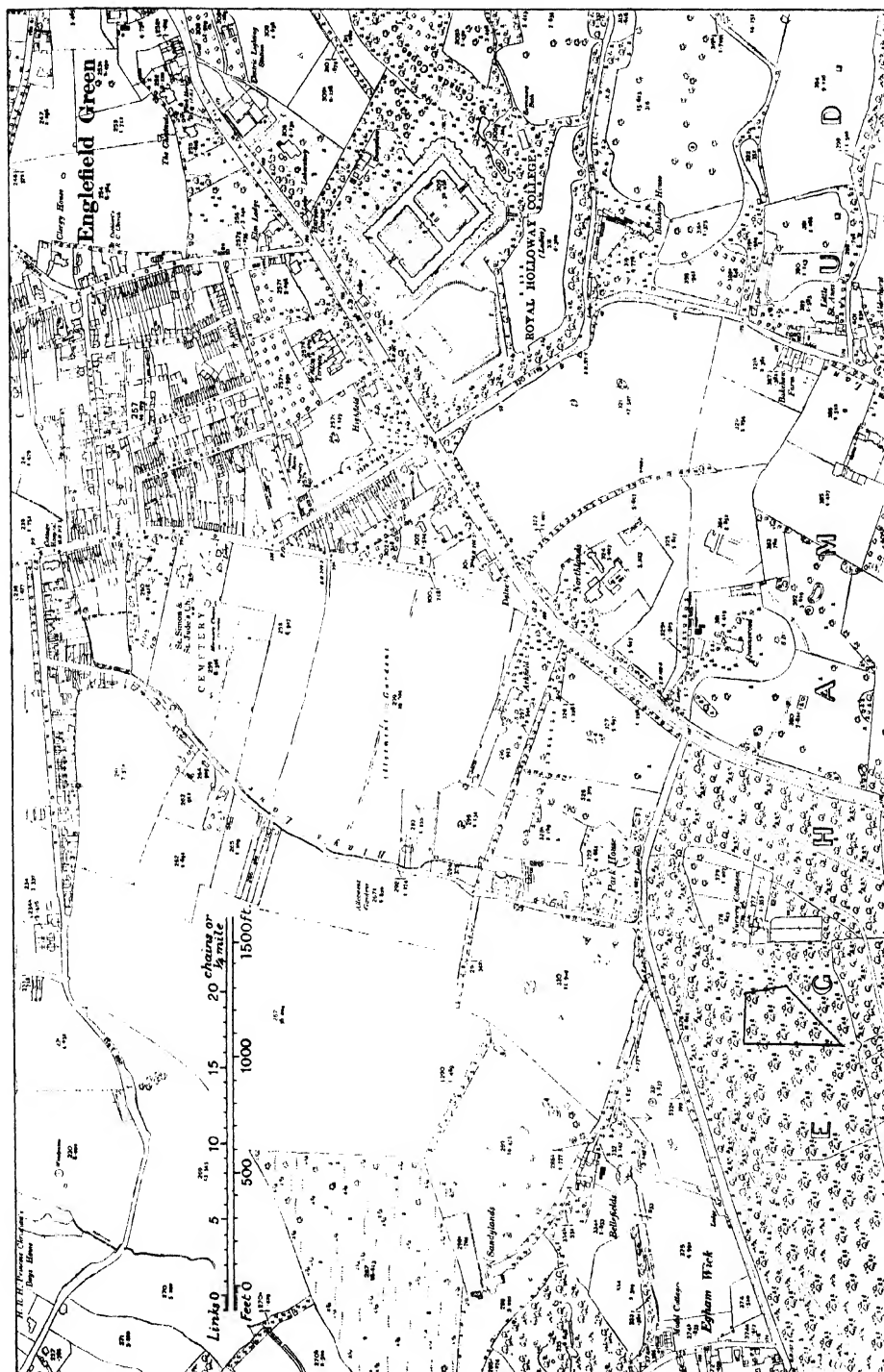


FIG. 1. Map showing the high road from Staines to Virginia Water with the Royal Holloway College.

lay humus composed of dead pine needles, twigs and cones, and then sand varying in depth from a few inches to 4 feet. In some parts, the water level was at the junction of the sand and the subjacent clay; in other parts it was in the sand. During the course of investigation, the level of the water table was found to vary with the seasons to a very marked degree.

At the south-east corner of the plot, there was a small bog, where the water, like that in the soil in other parts of the area, was acid to litmus. Species of *Sphagnum* and *Polytrichum* grew in the bog and at the edge were three species of *Juncus*. On the banks of the bog were numerous seedlings of *Betula alba* (*verrucosa*), and *B. pubescens*, *Pinus sylvestris*, *Castanea sativa* and *Rhododendron ponticum*.

Along the north-west of the area there was a fringe of vegetation. This consisted of pine and birch seedlings of the current season, *Molinia caerulea*, *Deschampsia flexuosa*, *Erica cinerea*, *E. tetralix*, and *Calluna vulgaris*, which had secured a hold owing to a slight opening in the forest in that region. Occasional seedlings of *Larix europaea*, *Ulex europaeus*, *Castanea sativa* and *Quercus robur* (*pedunculata*), also of the current year, were noted.

The charred patches, where fires had been made, were for the most part bare, but towards the centre of each patch *Funaria hygrometrica* was beginning to establish itself.

During the autumn of this year, a remarkable feature of the plot was the luxuriant growth of *Bulgaria polymorpha*, the sporophores of which reached a diameter of 5 or 6 inches in their spread over the soil. A very few individuals of wind-dispersed immigrants, such as willow herb, and even dandelion and thistle, had arrived. With these exceptions, the land was clear of vegetation, and thus might be said to offer a new habitat for colonisation.

METHOD

The area, comprising altogether some 4980 sq. ft., was divided into 46 smaller areas; peripheral areas 20 ft., 45 ft. and 60 ft. square, and central areas of greater size (Fig. 2). Quadrat charts were made of each in 1917, 1919 and 1924. Figs. 5-8 illustrate four out of the forty-six such series made. Each year general observations were recorded in note form, and plants observed were listed.

In addition to the mapping of the whole area intensive studies were made of features of special interest, e.g.:

(a) The extension of each patch of bracken was measured separately.

(b) An intensive study was made of certain subdivisions of the above areas, e.g. of the "oases."

(c) An intensive study of individual species was made with reference to depth of root in the soil.

The water table was observed at intervals by noting the height of water in the bog, which frequently became a pond, and by digging in other parts.

OBSERVATIONS MADE DURING 1918

Until the late autumn of 1918, the appearance of the ground remained almost unchanged, except that the burnt patches were covered with bright green vegetation, and stood out vividly from the surrounding stretch of bare ground. The striking contrast between these patches and the barren "desert" surrounding them, suggested "oases." It is on this account that we shall use this term in our reference to them. The vegetation of the oases consisted of *Marchantia polymorpha* and *Funaria hygrometrica*, which now covered the whole of their surface.

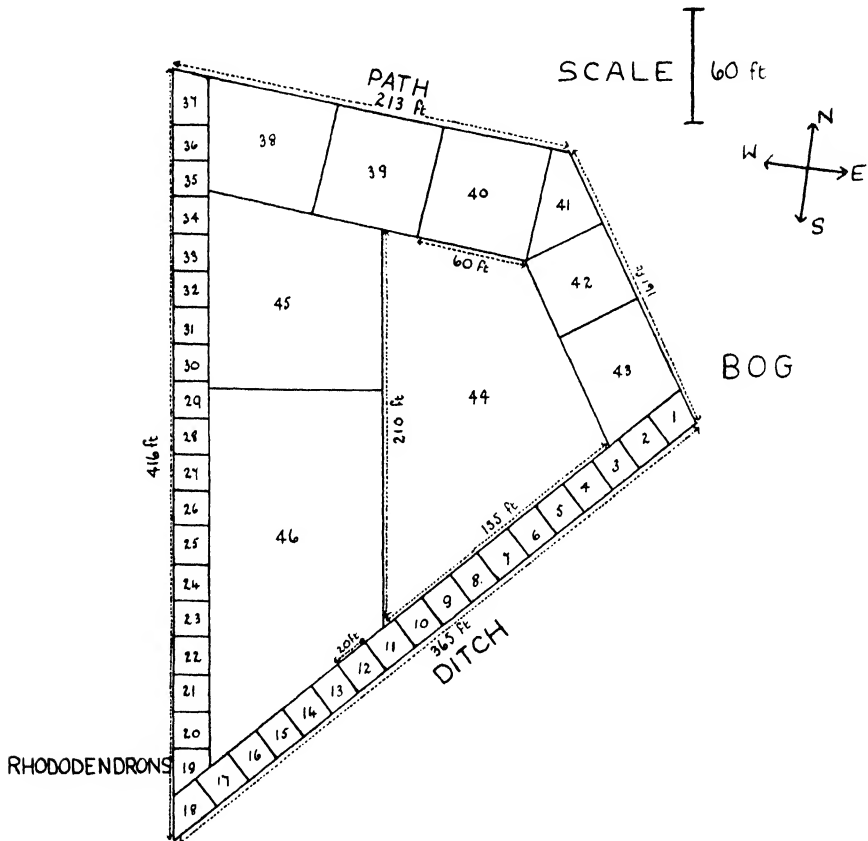


FIG. 2. Plan of the observational area divided into quadrats, etc. for map making.

Some evidence of a slight advance on the part of the peripheral vegetation was observed, and enumeration of seedlings gave a considerable increase of pines (*Pinus sylvestris*) and especially of birches (*Betula alba*).

The giant sporophores of *Bulgaria polymorpha* once again appeared, giving the area in some parts the appearance of being covered at short intervals with cow dung.

During this year rabbits were frequent visitors, as was seen by their nibbling of *Deschampsia flexuosa*, and by the gradually accumulating nitrogenous debris which they left behind them.

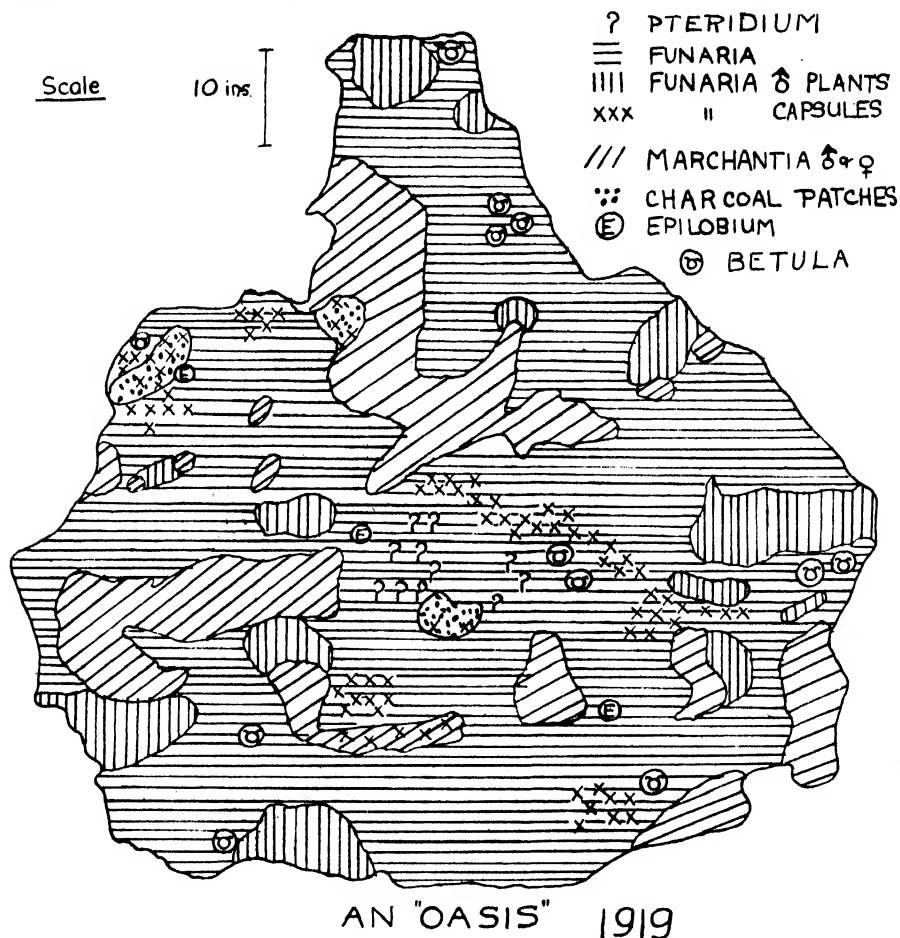


FIG. 3. Map of an oasis in 1919, illustrating the colonisation of a burnt patch.

OBSERVATIONS MADE DURING 1919

By May 1919, considerable changes had taken place, both on the open ground and on the oases (Fig. 3). The vegetation of the oases had a compact velvety appearance. Every square inch of space was occupied; indeed, in a few places the vegetation was stratified, for *Marchantia thalli* were found actually creeping over *Funaria*, and *Peltigera* was spreading horizontally over both. The *Marchantia*, which was very abundant, showed an unusually close formation of archegoniophores and antheridiophores, and was producing gemmae. *Funaria* was beginning to die down, and was covered with ripe capsules. In the centre of several of the oases, sporelings of bracken had made

considerable headway and were firmly established. Further interesting evidence of the oases being favourable seed beds was found in the variety of seedlings which had germinated upon them: for example, side by side were seedlings of a willow, a willow-herb, a holly, and a sheep's sorrel. It was most striking to find one bird-borne and three wind-borne individuals on a single oasis and only *one* example of each.

The central region of the area was almost as bare as in the previous year. As in the oases there were a few immigrants, which included two plants of clover, a few of chickweed, a few composites, and some poorly developed individuals of the rose bay willow-herb (*Epilobium angustifolium*).

In the peripheral region of the area *Molinia caerulea* was the dominant element in the vegetation, as the *Calluna* and *Erica* spp. and *Deschampsia flexuosa*, though slightly more abundant than formerly, had not increased at the same rate. Among the *Molinia* tussocks two year old birch seedlings were numerous and flourishing. The pine seedlings were fewer in number than the birches, and many of them looked unhealthy. As the result of excessive rain during the spring of this year, parts of the area were under water. The *Molinia* in these very wet parts was dead or dying.

In the bog, *Sphagnum*, although well supplied with water, was turning brown. The water in the bog was at this time neutral to litmus.

The summer of 1919 was dry, and in consequence the water table had receded, and the bog was almost dry. The increased aëration of the soil due to this change had favoured the progress of *Molinia*, which was, however, attacked by Ergot (*Claviceps purpurea*). At the outer limits of the area, with the exception of the ground immediately surrounding the tree stumps which was quite bare, *Molinia* was dominating an almost closed society.

On a few of the oases the vegetation had been uprooted and trampled down, and thus was not able to develop on natural lines. The damage was probably caused by rabbits. In the bog, *Sphagnum* had disappeared for the time being, *Polytrichum* had nearly disappeared, and a species of *Mnium* was replacing them.

No trace of *Bulgaria* was observed, although it had been so abundant the two previous autumns, nor has this fungus again appeared on the plot.

Throughout the area, various seedlings, many fungi, and a moss, *Campylopus flexuosus*, occurred occasionally, and served to break the otherwise uniform dark colouration of the bare regions.

OBSERVATIONS MADE DURING 1920

As the result of heavy rains during November and December 1919, the area was wet in the spring of 1920. In runnels washed out by the surface drainage during heavy rain, seeds of *Molinia* had germinated readily, and thus young *Molinia* plants occurred in straight lines as though produced by rhizomes. The *Molinia*, which was originally peripheral, now covered a

considerable part of the area. *Erica tetralix* and *Calluna vulgaris* were still associated with it, and were in a few localities even abundant. *Deschampsia* occurred frequently, but usually the foliage had been nibbled by rabbits. The pine seedlings were few in number, and unhealthy, except those on an elevated part of the bog margin.

Now for the first time were noted the ravages of the pine weevil in the pine stools; and it was found that some of the pine seedlings had been partly eaten. The birches on the other hand were very numerous, and some of them reached a height of five feet.

In October, *Sphagnum* appeared again in the bog. This was found to be coincident with a change in the bog water from neutral to acid reaction.

Some of the oases, though still velvety, had a different floristic content, for *Funaria* and *Marchantia* had been succeeded by *Dicranum longeanum*, a moss common on the Bagshot Sands. *Barbula fallax*, *Campylopus flexuosus*, *Hypnum purum* also occurred. The bracken on the oases was spreading rapidly, and appeared to be well established. As the *Molinia* advanced, it surrounded some of the oases, and eventually invaded them, the invasion being made easier no doubt by the previous breaking up of the surface by rabbits. The central part of the area was in parts dotted with young *Molinia* plants. A few specimens of species of *Erica*, *Calluna*, *Deschampsia*, and *Rumex* occurred, and *Campylopus flexuosus* was so prevalent, that in some places the ground was of a uniform green colour. No fruits of this moss were observed, but a method of propagation by detached branches, formerly recorded by Rabenhorst, may account for the rapidity of its distribution. If one draws a finger lightly over the surface of the moss, large numbers of short detached branches are thrust up, and lie free on the surface. This takes place so definitely, that one can mark out a design on the surface of the moss. These freely exposed branches can be blown away by the wind. If, on the other hand, the finger is drawn rapidly and with some slight pressure over the moss, the free branches spring up elastically, owing to the compressed condition of the upper stratum, as compared with that of the lower, and shoot to a considerable distance. Thus the scurrying of rabbits across a patch of *Campylopus* results in the wide distribution of leafy branches, which quickly establish themselves by rhizoids. This characteristic of *Campylopus* may account for its hold over the long exposed central region, which for some reason or other never became colonised by germinating seeds and spores.

OBSERVATIONS MADE DURING 1921

In the early part of this year, colonisation received a check as a result of fire. Many seedlings were scorched and birches injured and some of the pines completely destroyed. The injury to the *Molinia* was not fatal. Oases with their established bracken escaped, as *Campylopus* was incapable of spreading the fire. The bracken (*Pteridium aquilinum*) was growing radially out from

those centres where sporelings had previously been noted. There were only five oases on which bracken had failed to establish itself, and only five patches of bracken in places which had not formerly been burnt areas. Thus the great majority of established plants of bracken were strictly limited to the oases. On one of these *Marchantia* was growing well and bearing old archegoniophores.

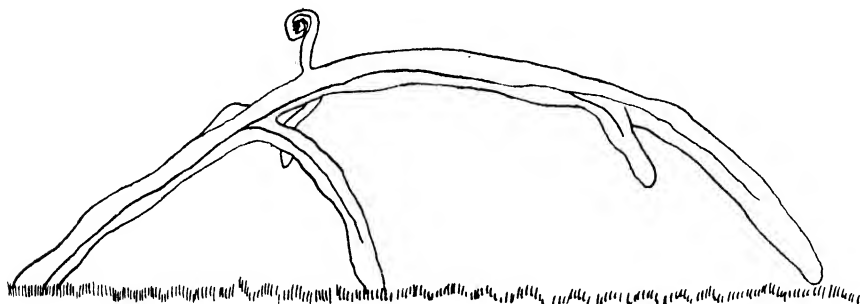


FIG. 4 (a). Arching of Bracken rhizome whose apex was unable to grow forward owing to the hardness of the soil. The portion of the rhizome behind the apex has elongated and curved, raising itself above the surface of the soil from which the apex has been lifted by hand.

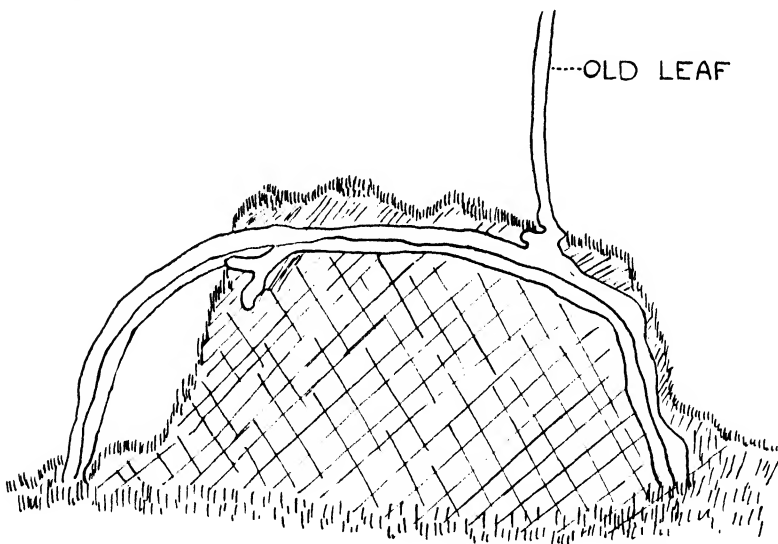
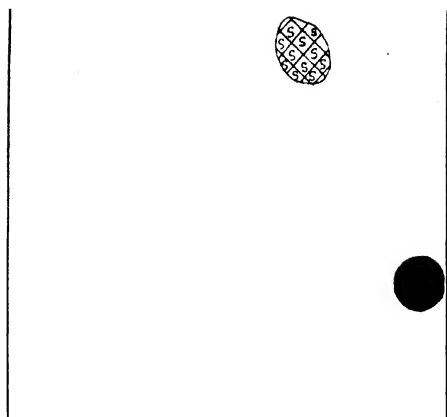


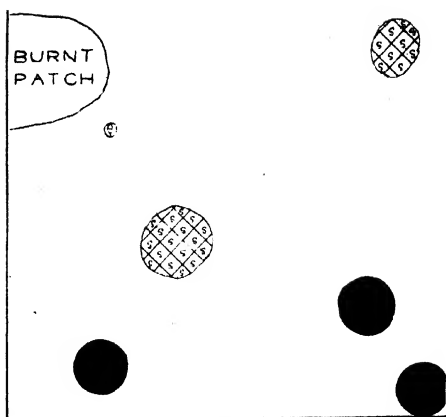
FIG. 4 (b). Arching of Bracken rhizome as in (a). Here the rhizome has raised the soil into a small hummock (indicated in section).

Another oasis was completely surrounded by *Molinia* and showed signs of yielding to its pressure, as *Polytrichum* was found brown and flattened under the tussocks.

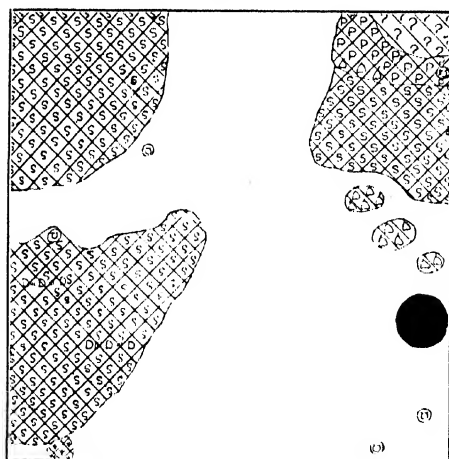
The summer was exceptionally hot and dry and there was much evidence of the ravages of rabbits. Both *Calluna vulgaris* and *Erica cinerea* were nibbled and the covering of *Campylopus*, so vividly green and uniform in 1920, was very thoroughly broken up into fragments. As the drought continued, *Campy-*



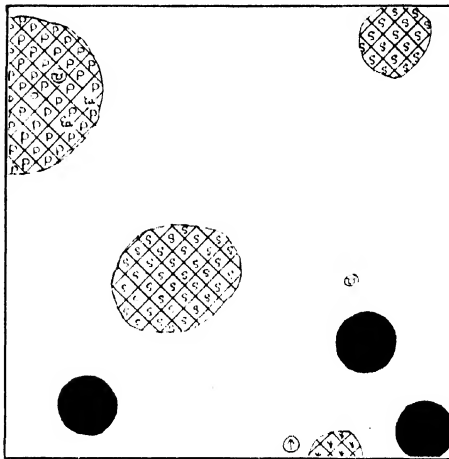
1917



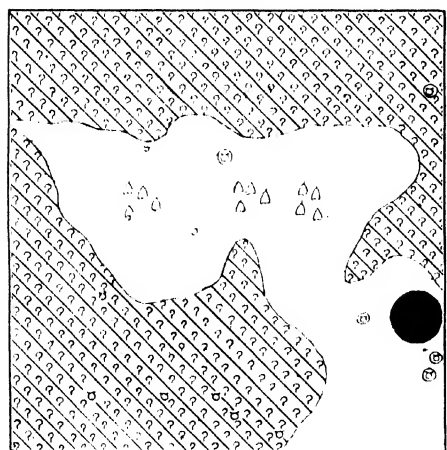
1917



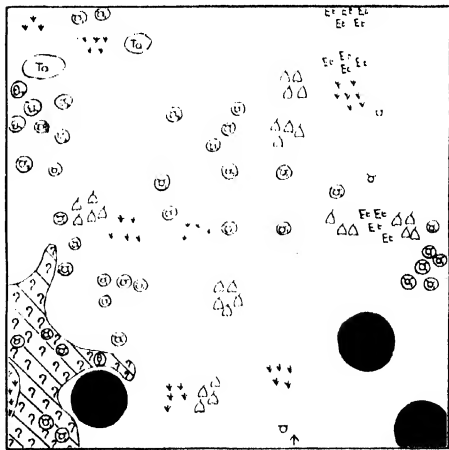
1919



1919



1924



1924

FIG. 5. Charts of quadrat 11 (20 × 20 ft.) in the years 1917, 1919 and 1924, illustrating the establishment of *Pteridium aquilinum* among Bryophyta.

FIG. 6. Charts of quadrat 14 (20 × 20 ft.) in the same years, illustrating the establishment of birches, *Betula alba* (verrucosa) and *B. pubescens*.

For key to symbols see page 129.

lopus was further destroyed, and by the end of the year a large central region of the observational area was again bare of vegetation. A deep hole dug in the south-west corner on June 10th had revealed no water even at a depth of three-and-a-half feet, though the sand became moist to the spade at a depth of nearly three feet.

It was evident in the autumn, that seedlings of *E. tetralix*, which had appeared among the *Molinia* plants in the north-east corner, were less affected by the drought than was *Molinia* itself. The rabbits had left the *Calluna* for the more succulent young birches and had nibbled leaves and dragged off the twigs up to a height of two or more feet. The bracken rhizomes on the oases were unable to continue their underground growth. In some cases the apex was still alive, in others it had perished but was still fixed in the ground, and where the apex had failed to progress, knee-like ascending curves were formed by the rhizomes in their growth (Fig. 4). It seemed that elongation of the rhizome had been taking place but not at the apex. To verify this a detailed map of one oasis made in May of that year was compared with the oasis in its autumn state, and a record was made of the change in extent of the bracken in the five months that had elapsed. It was found that not only was the extent reduced along many radii, but there had been no considerable addition along any radius.

Very little progress was made therefore in 1921 owing to the fire in January and the subsequent drought, which not only retarded but actually destroyed much of the early beginnings of growth. Indirectly these events caused the destruction of the lower branches of many birches, as the heather became too dry to be palatable to rabbits. During the following winter the rabbits did further injury to heather and birches and to the bracken, not only in its subterranean parts but in the newly exposed parts of the rhizomes (see Fig. 4).

A comparison with a neighbouring lumbered pinewood, viz. Callow Hill, was made in July. Here the vegetation had advanced much more rapidly. Nearly the whole hill side was covered with bracken, and there was much *Vaccinium myrtillus* and several young deciduous trees: *Rhamnus frangula*, *Quercus* sp. and *Castanea*. Oases which, three years previously, had been as

KEY TO FIGURES 5, 6, 7 AND 8.

●	OLD PINE STUMP	☒	MOLINIA CAERULEA
○	BETULA ALBA	☒	PTERIDIUM AQUILINUM
R	RHODODENDRON PONTICUM	☒	SPHAGNUM spp.
♂	QUERCUS ROBUR (PEDUNCULATA)	P	POLYTRICHUM COMMUNE
U	ULEX EUROPAEUS	Di	DICRANUM LONGEANUM
⊕ ⊙ ⊗ ⊙	SEEDLING PINE, ULEX, BIRCH AND OAK	III D III	DESCHAMPSIA FLEXUOSA
E c	ERICA CINEREA	T a	TARAXACUM VULGARE
☒	ERICA TETRALIX	ε a	EPILOBIUM ANGUSTIFOLIUM
☒	CALLUNA VULGARIS	ε h	EPILOBIUM HIRSUTUM

well delimited as those on the Virginia Water area, were no longer distinguishable from the surrounding land, which was carpeted with vegetation. Another neighbouring lumbered area, viz. the Clockcase Woods, was still covered in many parts with an almost pure growth of *Epilobium angustifolium*. Thus three areas once dominated by *Pinus sylvestris* were regenerating along different lines.

OBSERVATIONS MADE DURING 1922

As already stated, the *Campylopus* covering of the central and otherwise barren area had been destroyed by the drought in 1921. It was interesting therefore to note in January 1922 that the soil had become almost covered with lichens, chiefly *Cladonia* species and some *Peltigera*. A careful examination of the soil for the presence of earthworms was made but no trace of worms or their casts was found, even in the vicinity of the bordering paths.

The exceptionally hot early summer was followed by a cool and rainy season which was extraordinarily favourable to the regeneration of the area. The ripening of spores and seeds served further to promote it. The history of the selected oasis was continued. The records made in October showed that the rhizomes of the bracken now extended from the centre of the oasis to a distance of $14\frac{1}{2}$ feet. This indicates the favourable conditions for growth of bracken that prevailed during the latter part of the summer of 1922.

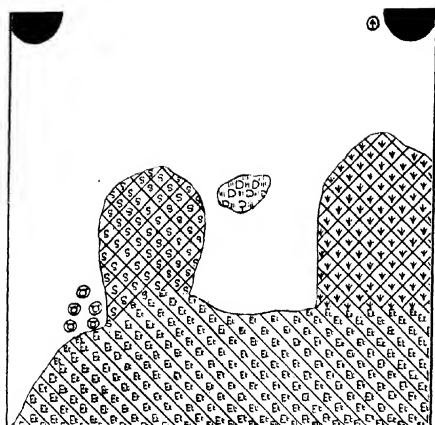
When 1922 closed the observational area looked quite overgrown and it was difficult to see the boundary. The tallest birches were six feet in height. There was still a considerable barren area in the centre: even the lichens which covered it in January had withered during the heat of the early summer.

The same rapid regeneration of the vegetation was observed in the two other lumbered areas during repeated visits made throughout the year. The development of their vegetation in 1922 accentuated the differences between them—differences not only floristic but also distributional. By means of contour maps the distribution of vegetation in all these areas was compared. From these it became evident that the inclined surface was always better populated than the flat surface above it, and less well populated than the flat surface below it, and this irrespective of aspect. It would appear either that the leaching of the plateau by rain was unfavourable to the establishment of new vegetation, or that the plateau periodically became too dry to support plant life.

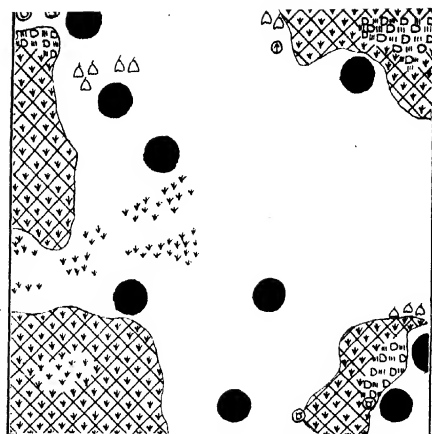
OBSERVATIONS MADE DURING 1923 AND 1924

In 1923 no records were made beyond the listing of plants that occurred in that year and the measuring of the bracken colonies.

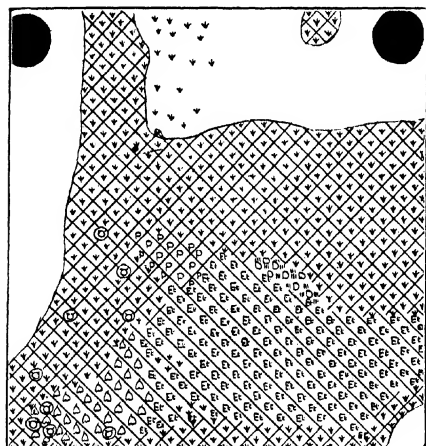
By 1924 the observational area was already a young birch wood (Fig. 6). The birches numbered some thousands and many had attained a height of 10 feet and more. There was still a bare region in the middle. Elsewhere the ground was covered with vegetation.



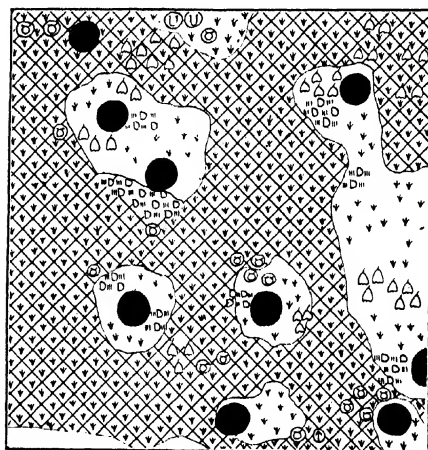
1917



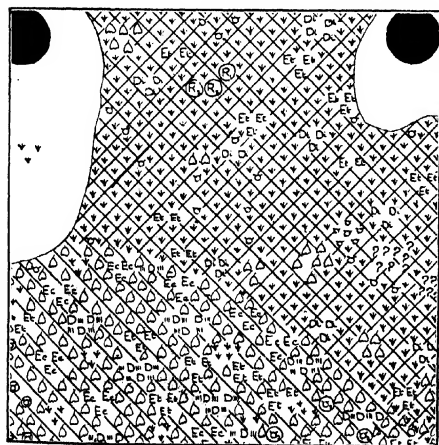
1917



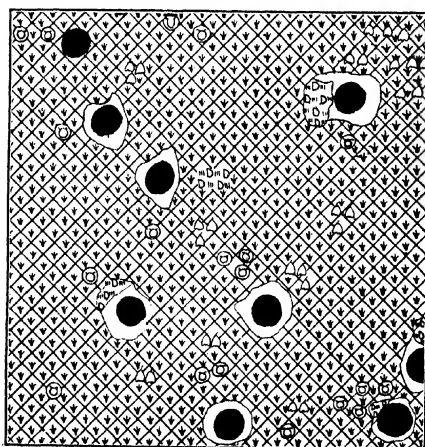
1919



1919



1924



1920

FIG. 7. Charts of quadrat 4 (20 × 20 ft.) in the years 1917, 1919 and 1924, illustrating the invasion by *Calluna vulgaris* of the already established *Erica tetralix*.

FIG. 8. Charts of quadrat 39 (60 × 60 ft.) in the years 1917, 1919 and 1920, showing the spread of *Molinia*.

For key to symbols see page 130.

Molinia caerulea and heaths, of which *Erica tetralix* was more abundant than *Calluna vulgaris*, were dominant and *Pteridium aquilinum* was locally dominant. There was no doubt that the steady progression of *Pteridium aquilinum* still continued. On the other hand *Calluna vulgaris* and *Erica tetralix* had often given way before encroaching *Molinia*. To a casual observer the grasses were the most noticeable feature of the ground flora, but in February 1925, when the birches and taller herbs were cut down by the forest authorities of Windsor Great Park, the equal dominance of the heaths was obvious.

Of the less frequently occurring members of the community, special mention must be made of young pines and rhododendrons, which occurred sporadically in the moister parts, that is along the ditch and near the bog. Twenty saplings of *Pinus sylvestris* and 103 seedlings of *Rhododendron ponticum* were counted. These numbers are explained by the fact that there were in the neighbourhood many rhododendron shrubs and a pine tree.

Other colonists recorded are:

ANGIOSPERMAE.

<i>Quercus robur</i> (pedunculata)	12	<i>Deschampsia flexuosa</i>	occ.
<i>Ulex europæus</i>	6	<i>Taraxacum vulgare</i>	occ.
<i>Ilex aquifolium</i>	1	<i>Urtica dioica</i>	2
<i>Rhamnus frangula</i>	5	<i>Rumex acetosella</i>	2
<i>Rubus fruticosus</i>	2	<i>Juncus communis</i>	occ.
<i>Erica cinerea</i>	occ.	<i>J. bulbosus</i>	
<i>Epilobium hirsutum</i>	occ.	(= <i>J. supinus</i> , Moench)	1

BRYOPHYTA.

<i>Sphagnum</i>	<i>Polytrichum</i>	<i>Dicranum</i>
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Old stumps of trees were found to be covered with lichens, e.g. *Parmelia fuliginosa* var. *laetevirens* and *Physcia ciliaris*, and mosses, e.g. *Hypnum cupressiforme* and *Ceratodon purpureus*.

The bare central region, which was higher than the rest and covered with a thin humus of pine needles, was colonised almost entirely by lichens and mosses which formed a close covering. *Cladonia maculenta*, *C. fimbriata* and occasionally *Peltigera canina* were found, and *Campylopus pyriformis* was frequent. Very rarely there occurred closely nibbled plants of *Calluna vulgaris*, and the less high regions around were sparsely covered with partly nibbled *Molinia caerulea*, untouched *Erica tetralix* and occasional *Festuca rubra*.

In order to discover how far the bareness of the central region was due to the ravages of rabbits, wire cages were set up in June 1924, each enclosing a square metre of ground; but no definite conclusions could be drawn from observation of these for they were unexpectedly destroyed six months later. In January 1925 the forest authorities of Windsor Great Park cut down the natural birchwood that had established itself on the observational area and replanted *Pinus sylvestris*.

LIST OF PLANTS RECORDED DURING 1917-1925

DICOTYLEDONS.

<i>Betula alba</i> (verrucosa)	<i>Quercus robur</i> (pedunculata)
<i>B. pubescens</i>	<i>Rhamnus frangula</i>
<i>Calluna vulgaris</i>	<i>Rhododendron ponticum</i>
<i>Castanea sativa</i>	<i>Rubus fruticosus</i>
<i>Cuscuta epithymum</i>	<i>Rumex acetosella</i>
<i>Epilobium angustifolium</i>	<i>Salix</i> sp.
<i>E. hirsutum</i>	<i>Senecio vulgaris</i>
<i>Erica cinerea</i>	<i>Taraxacum vulgare</i>
<i>E. tetralix</i>	<i>Ulex europaeus</i>
<i>Ilex aquifolium</i>	<i>Urtica dioica</i>
<i>Potentilla erecta</i>	

MONOCOTYLEDONS.

<i>Deschampsia flexuosa</i>	<i>Juncus bulbosus</i>
<i>Festuca ovina</i>	<i>J. communis</i>
<i>F. rubra</i>	<i>Molinia caerulea</i>

GYMNOSPERMS.

<i>Larix europaea</i>	<i>Pinus sylvestris</i>
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PTERIDOPHYTA.

<i>Pteridium aquilinum</i>

BRYOPHYTA.

<i>Marchantia polymorpha</i>	<i>Hypnum cupressiforme</i>
<i>Barbula fallax</i>	<i>H. purum</i>
<i>Campylopus flexuosus</i>	<i>Leucobryum glaucum</i>
<i>C. pyriformis</i>	<i>Mnium</i> sp.
<i>Ceratodon purpureus</i>	<i>Polytrichum commune</i>
<i>Dicranum longeanum</i>	<i>Sphagnum</i> spp.
<i>Funaria hygrometrica</i>	

FUNGI.

<i>Bulgaria polymorpha</i>	<i>Laccaria laccata</i>
<i>Calocera cornea</i>	<i>Merulius tremulosa</i>
<i>Claviceps purpurea</i>	<i>Mycena epipterigia</i>
<i>Flammula sapinea</i>	<i>Paxillus involutus</i>
<i>Galera hypnorum</i>	<i>Scleroderma vulgare</i>
<i>Hypoloma fastigiata</i>	

together with various species of *Phycomycetes* and *Myxomycetes*.

LICHENS.

<i>Cladonia fimbriata</i>	<i>Parmelia fuliginosa</i>
<i>C. maculenta</i>	<i>Physcia ciliaris</i>
<i>Peltigera canina</i>	

ALGAE.

Since 1919, a certain number of soil algae have been isolated, of which *Cystococcus* is the most frequent unicellular form and *Hormidium* the dominant filamentous. Perhaps the most interesting feature is the extraordinary abundance of *Carteria* from 1923 onwards, in the surface soil of the wetter parts.

DISCUSSION

The plant succession on the area passed through various stages of heath towards the establishment of a dense young birch-wood. In the centre of the

area even to the last (1925) there remained a bare region. The marked failure of all plants other than *Cladonia* spp. and *Campylopus* spp. to colonise here was striking. It could not be that seeds and spores did not arrive. It was at first attributed to the ravages of rabbits, but the isolation of a portion of the ground by means of cages of wire-netting did not, in the short period over which observations were made, justify this conclusion¹. The ground was higher here and its bareness may have been due to special conditions of leaching by rain or of extreme drought. The latter condition existed for short periods during the summer months, when the water table was very low. Possibly the area did not remain sufficiently moist for long enough at a time to allow seedlings and sporelings to become established. In addition to the lichen and moss mentioned above only occasional plants of *Calluna vulgaris* managed to get a hold; these were nibbled close by rabbits.

The failure of the pines to re-establish themselves may have been due, at least in part, to the attacks of the weevil which, by 1920, had become abundant among the pine stools. It is well known that weevils feed on young pines, and some pines had been attacked. No traces were ever found of the pine beetle (*Hylesmus piniperda*, L.), and this was due undoubtedly to the preliminary burning of the tree tops by the lumbermen. Apart from the weevil, disease and competition appear to have but little affected the vegetation, although ergot (*Claviceps purpurea*) occurred on *Molinia*, and dodder (*Cuscuta epithymum*) on *Calluna*. As natural regeneration of pines on the moister regions of the Bagshot Sands is known to occur, however, further explanation should perhaps be sought for their failure in this region. No less than 55 pine seedlings were counted in 1917, and 62 in 1919, but only 20 in 1924. These 20 surviving pines were all in the peripheral region of the area, on ground which had never been burnt or otherwise completely denuded. Fourteen of them are marked on the maps for 1917, 18 on the maps for 1919, and it is possible that the other two were overlooked. In 1925 they were well grown trees of 3 to 4 feet in height. Pine seedlings have rarely established themselves since the area was lumbered. It is evident that the ground is suitable for pines once they have established themselves, for the area has been successfully replanted with pines and was, of course, previously a pine-wood. Many suggestions might be offered to account for the failure: e.g. the possible loss by fire or drought of the essential symbiotic fungus of the roots, or the special character of coniferous wood, or the shallow root system of pine seedlings which could not withstand the periods of drought. Up to 1920 *Molinia* and *Betula* were the two Phanerogamic species which were best established on the area. The heaths had obtained a hold, but were not so abundant as *Molinia* and *Betula*.

In order to discover what characteristic of these plants made them more successful than any other colonists the root systems were compared with

¹ See note on page 137.

those of other species occurring on the area. It was found that two year old pine seedlings, *Erica*, *Calluna*, and *Deschampsia*, had root systems which ramified profusely in the humus, but did not penetrate the sand. In the case of two year old birches and *Molinia*, however, the roots reached the water level. These two species therefore were more capable of withstanding periods of drought, than were the shallow rooted plants. The establishment of the heaths on the area, in spite of their roots not tapping the water table, causes no surprise, for it is well known that the xerophytic character of their leaves enables the plants to thrive in difficult conditions of water supply. It is possible that the leaves of seedling pines are not so well equipped.

In the ravages caused by rabbits it is certain that *Calluna vulgaris* suffered most. *Erica cinerea*, *Molinia caerulea*, and *Deschampsia flexuosa* were often nibbled and in 1921, during the great drought, the rabbits left the dry *Calluna* for the more succulent young birch trees. *Erica tetralix* on the other hand was absolutely untouched. The preference shown by rabbits for *Calluna vulgaris* was very marked. This preference was an independent observation during the course of this work. We have since noted with interest that Farrow, in his work on the vegetation of Breckland (This JOURNAL, 5), has observed the same thing. In some parts, however, in spite of this, *Calluna vulgaris* steadily invaded the already established *Erica tetralix* (Fig. 7).

Among the problems which interested us was the scarcity of the Rose bay willow-herb (*Epilobium angustifolium*). The fact that only two flowering specimens of "Rose bay," or as the Canadians call it, on account of its presence after forest fires, "Fire weed," have ever been observed on the plot, has caused surprise. Its complete failure to establish itself is especially interesting on account of its wide occurrence on a similar lumbered region, called the Clockcase Woods, about a quarter of a mile distant on the south side of the Bagshot road. Rose bay grows abundantly on this land, and is spreading vegetatively, and by seed. The Clockcase Woods are on higher ground than the observational plot, and also on a steeper slope. The water table in the Clockcase Woods was 4 ft. 3 ins. below the surface, as compared with 20-30 inches in the Virginia Water area, when measured in November 1920. This level coincided with the level of the surface of the clay in the latter area, but, at a depth of $4\frac{1}{2}$ feet, no clay was found in the Clockcase Woods. Probably these differences unite to ensure in the soil of the Clockcase Woods a better drainage system, and more efficient aëration and nitrification than are found in that of the Virginia Water area. The Swedish botanists regard the Rose bay as a good index of active nitrification in forest soils. It is suggested that these factors may account for Rose bay occurring so abundantly in the Clockcase Woods, and so rarely in the other area.

With reference to the record of *Marchantia*, we may note that, while *Lunularia* and *Pellia* are extraordinarily abundant in the near neighbourhood of the College, *Marchantia* has always been scarce, and no member of the

College has known it to fruit in this district. The sudden appearance on the area of plants which were fruiting so abundantly that the ground was yellow with the shed spores caused, therefore, no little surprise. But the arrival of the plant was hardly more extraordinary than its almost total disappearance after two years of apparently successful establishment. The latter phenomenon may perhaps be partly accounted for by the sharp competition which occurred on the oases.

The sudden appearance of *Bulgaria polymorpha* in 1917 was not so surprising, for it is a common fungus in the neighbourhood. Its enormous size and its abrupt and complete disappearance were, however, most remarkable. It has not been recorded for the area since 1918.

SUMMARY

1. An account is given of the colonisation of a denuded area, the observation of which extended over eight years, viz. from the complete destruction by felling of a pine-wood in 1916, to the destruction in 1925 of a young birch-wood which had established itself in its place.

2. The establishment of a birch-wood on the waste ground of a destroyed pine-wood was due to two factors:

(a) The failure of *Pinus sylvestris* to re-colonise the ground: pine seedlings numbered 55 in 1917, 62 in 1919 and 20 in 1924.

(b) The immense success of *Betula alba* both in growth of each individual (many had attained ten feet in height by 1925), and its quick increase in number (birch seedlings numbered 53 in 1917, 219 in 1919 and over 1000 in 1924).

3. In the record by notes and maps made from year to year of the evolution of the birch-wood further facts of general interest made themselves evident:

(a) The immediate colonisation of certain burnt patches of ground by *Marchantia polymorpha* and *Funaria hygrometrica*.

(b) The establishment of *Pteridium aquilinum* in these moist nests of Bryophyta.

(c) The steady advance of the *Pteridium* from these definite centres over the surrounding, usually bare, ground.

(d) The widespread colonisation of the area by numerous individuals of *Betula alba*, *Molinia caerulea*, *Erica tetralix* and *Calluna vulgaris*.

(e) The competition between *Molinia* and the heaths, which, to the casual observer in 1924, appeared to be won by *Molinia*, although, as was clearly seen after the cutting down of the vegetation in 1925, neither could be considered dominant.

(f) The competition between *Calluna vulgaris* and *Erica tetralix*, in which the latter became dominant on the moist parts and the former on the high and dry parts; in which too the latter had an advantage in being distinctly more successful in the early years.

(g) The obvious preference shown by rabbits for the *Calluna*.

(h) The striking absence of angiosperms other than the few mentioned above, especially of *Epilobium angustifolium*, which in other regions was locally dominant in similar denuded and burnt areas.

4. Certain facts of special interest emerged:

(a) The outcrop of immense sporophores of *Bulgaria polymorpha* in the first two years, and its total absence since 1918, although other fungi, lichens and mycetozoa were numerous on the ground and on the old tree stumps.

(b) The luxuriance of *Marchantia polymorpha* in 1919, especially rich in archegoniophores, antheridiophores, and gemmae, and its total disappearance later, along with its fellow pioneer *Funaria hygrometrica*.

(c) The special method of dispersal of the moss *Campylopus flexuosus*, which ensured its widespread success until the drought in 1921.

(d) The peculiar knee-like curves of the lengthening rhizomes of *Pteridium aquilinum*, whose growing points were prevented from advancing in the hard ground after the drought in 1921.

Acknowledgments are due to our colleagues N. Thomas (Mrs Ferguson) 1917–1919, and K. E. Light 1919–1925, and to students in the Botany School, Royal Holloway College, during the years 1917–1925. The figures have been drawn by M. I. Thomas.

NOTE ADDED JANUARY, 1926.

It is now possible to make a more definite statement with regard to the influence of rabbits on the bare central region.

Before replanting with pines in January, 1925, the forest authorities enclosed the whole area by rabbit-proof fencing. In the autumn of that year it was observed that the central region was becoming colonised to some degree. The occasional old plants of *Calluna vulgaris* were no longer closely nibbled and new plants had established themselves. Photographs taken from the same spot in June, 1924, and October, 1925, show a noticeable increase in vegetation in the central region. Destruction by rabbits, therefore, was one factor responsible for the continued failure of vegetation to colonise the central region during the eight years the area was under observation.

ON THE ORIGIN OF THE XEROTHERMIC PLANT ELEMENT IN BULGARIA

By N. STOYANOFF.

The vegetation of Bulgaria has been often described as being of a steppe character. Such terminology may be found both in descriptions by well-known travellers and in contemporaneous geographical manuals. Although partly exaggerated these descriptions correspond to a certain extent with the opinion of several phytogeographers. Thus, Velenovsky¹ describes as a steppe the environs of Rahovo and Burgas, and Podpera² those of Khaskovo. However, after studying carefully the vegetation of such woodless localities in Bulgaria, it becomes evident that this steppe character is hardly natural. Even in such especially treeless districts as the environs of Gebedje in eastern Bulgaria, numerous remnants of a former forest vegetation may be observed in the form of reduced shrubs of *Quercus pubescens*, *Ulmus campestris*, *Carpinus duinensis*, *Fraxinus ornus*, *Acer campestre*, etc. Here and there even separate small trees are yet preserved. In the above mentioned localities near Rahovo, Burgas and Khaskovo such remnants of a former forest vegetation are rather more evident. The country between Sofia and Dragoman, which Lavelyé³ describes as a real steppe, was covered in historic times with large forests, which formed a part of the famous *Sylva bulgarica*, renowned in the history of the Crusades. Remnants of the forest vegetation, which composed these woods, are even comparatively abundant to-day. The forests of Deli-Orman in north-eastern Bulgaria are the last remains of the natural vegetation, which once covered the now nearly woodless plain of the Danube.

The present lack of trees and the spreading of the steppe plants in many parts of Bulgaria are chiefly due to the direct and indirect activities of man.

Adamovič⁴ gives a true and instructive description of how wooded areas in Bulgaria and the neighbouring countries are gradually transformed into scrub-land by man and his methods of farming. Afterwards the bushes disappear also and the terrain becomes like a real steppe.

The plants, spreading through such deforested terrains, belong mostly to xerothermic species, such as are able to spread rapidly and to accommodate themselves easily to new conditions. Their dispersal is indirectly aided by man,

¹ J. Velenovsky. *Flora bulgarica. Suppl.* 1, 324-327.

² J. Podpera. "Ein Beitrag zu den Vegetationsverhältnissen in Südbulgarien." *Verhandl. d. zool.-bot. Ges.* p. 608. Wien, 1902.

³ E. de Lavelyé. *La péninsule des Balkans*, pp. 56-58. Bruxelles, 1886.

⁴ L. Adamovič. *Die Vegetationsverhältnisse der Balkanländer*, pp. 526-528. Leipzig, 1909.

and increases with the enlargement of the cultivated surface. Many of them belong to the ruderal and half-ruderal element.

Representatives of such a secondary steppe vegetation are:

<i>Andropogon ischaemum</i>	<i>Melilotus officinalis</i>	<i>Veronica spicata</i>
<i>A. gryllus</i>	<i>Astragalus onobrychis</i>	<i>V. teucrium</i>
<i>Cynodon dactylon</i>	<i>Coronilla varia</i>	<i>V. chamaedrys</i>
<i>Poa bulbosa</i>	<i>Linum perenne</i>	<i>Plantago lanceolata</i>
<i>Bromus erectus</i>	<i>Polygala comosa</i>	<i>P. arenaria</i>
<i>Festuca ovina</i>	<i>Euphorbia virgata</i>	<i>Asperula cynanchica</i>
<i>Aegilops cylindrica</i>	<i>E. gerardiana</i>	<i>A. galioides</i>
<i>Carex praecox</i>	<i>Eryngium campestre</i>	<i>Galium verum</i>
<i>Polygonum convolvulus</i>	<i>Bupleurum falcatum</i>	<i>Scabiosa ucranica</i>
<i>Silene otites</i>	<i>Falcaria rivini</i>	<i>S. ochroleuca</i>
<i>Stellaria graminea</i>	<i>Nonnea pulla</i>	<i>Campanula trachelium</i>
<i>Cerastium arvense</i>	<i>Onosma</i> spp.	<i>C. bononiensis</i>
<i>Holosteum umbellatum</i>	<i>Ajuga genevensis</i>	<i>Achillea millefolium</i>
<i>Herniaria glabra</i>	<i>A. laxmanni</i>	<i>A. setacea</i>
<i>H. hirsuta</i>	<i>Teucrium polium</i>	<i>Artemisia campestris</i>
<i>Sanguisorba minor</i>	<i>Salvia silvestris</i>	<i>Centaurea</i> spp.
<i>Potentilla recta</i>	<i>S. aethiopsis</i>	<i>Tragopogon majus</i>
<i>P. argentea</i>	<i>Stachys germanica</i>	<i>T. orientalis</i>
<i>P. canoscens</i>	<i>S. recta</i>	<i>Lagoseris bifida</i> , etc.
<i>Medicago falcata</i>	<i>Verbascum</i> spp.	
<i>M. minima</i>	<i>Linaria genistaeifolia</i>	

In some parts of South Bulgaria, as for example around Khaskovo, the presence of numerous Papilionaceae and among them especially of different species of *Trifolium* is characteristic for such pseudo-steppe formations. A similar spreading of the xerothermic elements, due to the activities of man, has been observed also in other countries of Europe. It is noted in the Western Alps by Briquet¹, in Germany by Weber² and Schalow³, etc.

Simultaneously with this secondary steppe vegetation traces of a primeval xerothermic plant element may be observed in Bulgaria. It differs from the above described in several respects. It is neither able to spread extensively, nor to accommodate itself to any new ecological conditions created by man. Its components are therefore generally distinguished by their conservative character and may be met here and there in localities which are little influenced by cultivation and probably were not wooded even in those times when Bulgaria was more forested than it is to-day. Refuges or relict-places of such plants may be chiefly found on dry limestone rocks, less often on other kinds of dry rocks, on sand, salty soils, etc. Such a characteristic refuge may be observed on the rocky limestone hills between Dragoman and Belidie in Western Bulgaria. On these hills there are growing:

<i>Stipa pennata</i>	<i>Amygdalus nana</i>	<i>Eryngium palmatum</i>
<i>Agropyrum cristatum</i>	<i>Astragalus testiculatus</i>	<i>Hyssopus officinalis</i>
<i>Allium saxatile</i>	<i>A. depressus</i>	<i>Goniolimon tataricum</i>
<i>Silene longiflora</i>	<i>A. pubiflorus</i>	<i>Artemisia camphorata</i>
<i>Anemone silvestris</i>	<i>Anthyllis montana</i>	<i>Jurinea tsar-ferdinandi</i> , etc.
<i>Potentilla rupestris</i>	<i>Cachrys alpina</i>	

¹ J. Briquet. "Le développement des Flores dans les Alpes occidentales." *Résult. scient. du Congrès Internat. Botan.* pp. 166-167. Vienne, 1905.

² A. Weber. "Die Geschichte der Pflanzenwelt des norddeutschen Tieflandes seit der Tertiärzeit." *Ibid.* p. 111.

³ E. Schalow. "Die Pflanzenverbreitung und vorgeschichtliche Besiedelung." *Naturwiss. Wochenschr.* pp. 173-177, 1922.

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Another similar oasis with evidently old xerothermic vegetation lies on the limestone rocks and calcareous sands near Gebedje, in Eastern Bulgaria. Of the xerothermic plants, which occur there, may be mentioned:

<i>Silene supina</i>	<i>Lepidotrichum uechtritzianum</i>	<i>Hedysarum tauricum</i>
<i>Gypsophila paniculata</i>	<i>Astragalus virgatus</i>	<i>Ruta biebersteinii</i>
<i>Arenaria rigida</i>	<i>A. austriacus</i>	<i>Matthiola tristis</i>
<i>Thymus carnosulus</i>	<i>A. vesicarius</i>	<i>Salvia grandiflora</i> , etc.
<i>Linum flavum</i>	<i>A. albicaulis</i>	

Refuges of conservative xerothermic plants may be observed also in many localities, spread almost over the whole surface of Bulgaria. As representatives of this type of vegetation the following species may be listed:

<i>Ephedra vulgaris</i>	<i>Saponaria bellidifolia</i>	<i>Anthyllis aurea</i>
<i>Stipa aristella</i>	<i>Queria hispanica</i>	<i>Polygala supina</i>
<i>S. capillata</i>	<i>Minuartia montana</i>	<i>P. rhodopea</i>
<i>Bromus transsilvanicus</i>	<i>Iberis saxatilis</i>	<i>Pimpinella tragium</i>
<i>Brachypodium sanctum</i>	<i>Spiraea crenata</i>	<i>Androsace maxima</i>
<i>Psilurus nardoides</i>	<i>Caragana frutescens</i>	<i>Verbascum humile</i>
<i>Lepturus pannonicus</i>	<i>Astragalus physocalyx</i>	<i>Celsia orientalis</i>
<i>Sternbergia colchiciflora</i>	<i>A. pugioniferus</i>	<i>C. roripifolia</i>
<i>Asphodeline taurica</i>	<i>A. thracicus</i>	<i>C. rupestris</i>
<i>Allium flavum</i>	<i>A. jankae</i>	<i>C. bugulifolia</i>
<i>Silene chlorantha</i>	<i>A. arnacantha</i>	<i>Morina persica</i> , etc.

A recent extension of most of the above xerothermic plants can hardly be postulated. Most of them cannot withstand the influence of cultivation, and disappear in localities to which farming extends. Practically none of them shows any tendency to increase the area of its distribution in Bulgaria, at least under the present physical conditions. Some of them show features characteristic of relict organisms, whilst they do not reproduce freely. Some of them even seem to be on the way to extinction in Bulgaria. *Astragalus physocalyx*, an old type, belonging to the monotypic Section *Pogonotropis*, is a good example. The only place, where this plant was known to grow, was on a rocky hill near Philippopol. Even in 1871 Janka, after a long search, could find only a single group of 10 specimens of this plant¹. He stated then, that only a few of the fruits he found on these plants seemed to produce viable seed. During the last 17 years *Astragalus physocalyx* has not been found, either in that place or elsewhere, and the only two living specimens, known at present, are growing in pots in the Royal Botanic Garden in Sofia. All attempts to multiply this species were unsuccessful, because ripe fruits of it can be rarely obtained. *Jurinea tsar-ferdinandi*, growing on the limestone rocks near Dragoman, does not seem to flower every year, and even when it does, the flowers and fruits are usually not abundant. *Astragalus testiculatus*, which also grows near Dragoman, seems similarly to have only slight powers of reproduction.

Many of the plants listed above have a limited distribution in Bulgaria,

¹ V. Janka. "Correspondenz aus Philippopol" in *Oesterr. bot. Zeitschr.* p. 218, 1871.

being known only in one or two isolated localities. Thus *Cachrys alpina*, *Astragalus testiculatus*, *Paeonia corallina* and *Artemisia chamaemelifolia* are each known from only one locality in Western Bulgaria, *Iberis saxatilis*, *Astragalus arnacantha* and *A. jankue* each from one locality in Southern Bulgaria, *A. pubiflorus* in two isolated places in Western and Eastern Bulgaria, *Alsine montana* in one place in Bulgarian Macedonia. *Brachypodium sanctum*, *Asphodeline taurica*, *Polygala supina*, *Verbascum humile*, etc. are growing in discontinuous and isolated areas.

The existence of relict xerothermic plants, which may be found in several isolated places, dispersed over almost the whole surface of Bulgaria, supports the opinion, that Bulgaria has passed through an era of time when xerothermic plants were more widely spread than they are at present and when the climate was relatively drier. That era probably corresponds with the period when in Northern Bulgaria the thick layers of loess were formed, which are so characteristic of this part of the country. It was probably the time which is described by geologists for Middle Europe as the Aquilonar or Steppe period.

A similar twice repeated spreading of the steppe vegetation has been observed also in neighbouring countries. Thus in Southern Russia, according to Kusnezow¹, the steppe vegetation has enlarged its area within historic times, in consequence of the destruction of forests by man. In prehistoric times the forests had advanced southwards over the steppe. However, traces are found also of an old wider spreading of steppes, which preceded the natural extension of forests in Southern Russia.

In that more remote period there probably occurred in Bulgaria the extensive development of certain plant genera such as *Genista*, *Astragalus*, *Verbascum*, *Centaurea* and certain sections of *Dianthus*, which are now represented by numerous species. Some of them seem to have continued this development till the present time; some others, such as *Verbascum*, are now represented by mostly constant and well limited forms.

If we examine the geographical distribution of this xerothermic vegetation, it becomes evident that it has a considerable and direct connection with the steppe vegetation of Southern Russia. How intimate this connection is may be illustrated by the fact, that of 425 species, which Krasnov² refers to as characteristic of the South-Russian steppes, 272, i.e. more than 60 per cent., occur also in Bulgaria. Besides this there is a noteworthy connection also with the Mediterranean flora, as has been observed by all investigators of the Bulgarian flora.

In many cases xerothermic plants are so widely spread both in the Mediter-

¹ N. J. Kusnezow. "Die Vegetation und die Gewässer des Europäischen Russlands" in *Engler's bot. Jahrb.* Bd. 28, 221-222, 1899-1901.

² A. Krasnov. "Steppes de la Russie méridionale." *Annales de géographie*, 111, 315-318, 1894.

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anean and the Steppe provinces, that it is difficult to decide to which group they may belong. As examples may be mentioned:

<i>Stipa pennata</i>	<i>Salvia aethiopis</i>	<i>Triticum cristatum</i>
<i>S. capillata</i>	<i>Scutellaria orientalis</i>	<i>Ephedra vulgaris</i>
<i>Phleum boeheimeri</i>	<i>Chondrilla juncea</i>	<i>Asparagus officinalis</i>
<i>Crypsis alopecuroides</i>	<i>Erysimum repandum</i>	<i>Allium moschatum</i>
<i>Euphorbia gerardiana</i>	<i>Eryngium campestre</i>	<i>A. flavum</i>
<i>Teucrium polium</i>	<i>Androsace maxima</i>	<i>A. paniculatum</i> , etc.

The South-Russian steppes, whose vegetation is so closely related to the Bulgarian xerothermic plant elements, are a relatively new formation, geologically speaking. Their flora is consequently also of a relatively new origin and received its elements from the neighbouring countries, after the recession of the sea, which formerly covered that province.

Only a very small proportion of the steppe plants can be supposed to have originated in Southern Russia itself. Krasnov mentions 16 species, which he supposes to be endemic and original elements of that vegetation. These plants are growing in the most elevated parts of the South-Russian steppes, on areas of soil which, according to the Russian geologists, have not been covered with water, but formed islands in the Quaternary South Russian Sea. This statement of Krasnov's received lately an indirect affirmation by Kuzniar's investigations¹. This author found in Southern Russia traces of an old mountain range, which ran in the direction—from Volhynia and Podolia, across Jitomir and Ekaterinoslav towards the estuary of the Don. This mountain range was connected by extensions with the Crimea and Caucasus and also with the Dobruja, i.e. with the eastern part of the Balkan Peninsula. Szafer² records Tertiary relict plants in the vegetation of Volhynia and Podolia, whose presence is connected with the history of that mountain range. It is therefore interesting that of the 16 species mentioned by Krasnov as relicts, one is related to a species known from the Balkan Peninsula and one is recorded from Bulgaria. *Schiwerekia podolica* is represented in the mountains of the Balkan Peninsula by a closely related species—*S. bornmulleri*, while *Asperula tyraica* is recorded from Bulgaria.

South Russia is, from the geographical point of view, only an advanced post of the large steppes and deserts of Western and Central Asia, hence the closest relationship between the vegetation of these countries is to be expected. Such relationship is accepted as a matter of course by many floristic investigators. An especial light is thrown on the character of this relationship by the conclusions reached by Borszczow³, whose knowledge of the steppe vegetation in European and Asiatic Russia is above all doubt. These conclusions are summarized by him in the following six points:

(1) The majority of the commoner plants of Central Russia with a distribution west of the Caspian Sea, extending to Transcaucasia, have as their

¹ According to **W. Szafer**: "Les plantes tertiaires montagnardes sur la chaîne scythique dans le refuge de Podolie et Volhynie." *Acta Societ. botan. Poloniae*, **1**, 97–119, 1923.

² *L.c.*

³ See **O. Paulsen** cited below.

southern limit of distribution east of the Caspian Sea in Aralo-Caspia, the parallel of $51\frac{1}{2}^{\circ}$ N. lat.

(2) When these forms occur farther east in Siberia, the boundary limiting their area of uninterrupted distribution lies outside of Aralo-Caspia and always north of $51\frac{1}{2}^{\circ}$ N. lat.

(3) *Most of the typical steppe plants met with in Southern Russia, and distributed towards the west from the Caspian to the foot of the Caucasus, attain their southern limit in Aralo-Caspia at the parallel of 49° N. lat. and their eastern boundary at the meridian of the Mugodshar range; if they occur farther east, they never go farther south than 49° N. lat.*

(4) The more southern plant forms, characteristic both for Persia and Aralo-Caspia, do not occur in our flora of the present time farther north than 49° N. lat.

(5) The more eastern forms, met with in the Altaian Siberia, are rarely met with farther west than 78° E. long. F. (about 60° E. Greenwich).

(6) In the case of a great many south-eastern forms, the lower course of the Syr-Daria ($45-46^{\circ}$ N. lat.) is the northern boundary and the meridian of the eastern shore of the Aral Sea (70° E. long. F.—about 62° E. Greenwich) forms the western boundary¹.

If we trace on a geographical map the boundaries mentioned by Borszczow, becomes evident, (1) that the steppe flora in South-Eastern Europe has relatively little in common with the xerophytic vegetation of Turkestan and Central Asia; (2) that a flora, related to that of the steppes in South-Eastern Europe, occurs in Western Siberia only in a tract of land which lies between 49° N. lat. and the belt of the Siberian forests. These facts scarcely harmonize with the common conception of the South-Eastern European steppes as only a branch of the large steppes and deserts of Asia. However, almost the same conclusions have been reached by modern Russian botanists. Thus according to Kuznezov², the steppes of Western Siberia occupy a tract of land, whose northern boundary runs across Jalutorovsk, Ishim, Tatarskaia, Kolivan, then makes a bend at the foot of Altai, across Kusnetsk, Biisk, Lokotievsk, takes a direction towards the south-east, along Irtysh and the Lake Zaisan-Nor and reaches Western Mongolia. Their southern boundary lies on the watershed between the Arctic Ocean and the Aralo-Caspian basin. South of this watershed are spread the steppes and deserts of Turkestan, whose vegetation belongs, according to Korzinsky, to another type, namely to a southern or subtropical flora.

It is difficult to say what kind of historical relationship exists between the steppe flora of South-Eastern Europe and that of the above described relatively

¹ According to O. Paulsen. "The Second Danish Pamir Expedition, conducted by O. Olufsen." *Studies on the Vegetation of the Transcaspian Lowlands*, pp. 29-30. Copenhagen, 1912.

² N. J. Kuznezov. "Essai d'une division de la Sibérie en provinces phytogéographiques." *Bulletin de l'Acad. Imp. des Sciences de St. Pétersbourg*, pp. 894-895, 1912.

narrow tract of land in Western Siberia. The few geological facts known about Western Siberia give no clear answer to this question. However, there are few grounds for supposing that a centre of development for xerothermic vegetation lay in that part of Siberia. According to the geological investigations, the Caspian Sea was connected with the Arctic Ocean even to the beginning of the Glacial period. Published opinions are contradictory as to whether this connection was across Western Siberia or across the eastern part of European Russia. Most of the geologists agree that large water basins occupied Western Siberia, north of the watershed between the Arctic and the Aralo-Caspian, up to the beginning of Post-glacial times. Even at present small water basins are extremely abundant over the whole of the West-Siberian steppes. More than 200 lakes may be seen within the limits which Kuznezov traced for these steppes, by examining even a relatively small map of Asia¹. There is no doubt that these water basins formerly had a notably larger extent than they have to-day. Thus Krilov² proves that a large lake existed within the present Barabinskaia steppe. H. Printz³ found in the Siberian steppes remnants of a former tundra vegetation, which he attributes to the Glacial period. As Krilov proves, no evidence exists that the steppe vegetation in Western Siberia was formerly wider spread than now, i.e. Western Siberia has not had in the past a "Steppe period," analogous to that which is generally accepted for Middle and Eastern Europe. All the conclusions on the existence of such a Steppe period in Western Siberia are founded, according to him, on erroneous analogies with Europe and erroneous generalisations based on fossil animal finds⁴.

The steppe vegetation of Western Siberia seems therefore to be of relatively new origin and was probably first developed in its present form in the Post-glacial epoch. On the other hand, as Penck⁵ showed, steppes were widely spread in Middle and Eastern Europe at the end of the Inter-glacial and during the last glaciation (only two Glacial periods being admitted for those regions which are at a certain distance from the area of the main glaciation). It may be supposed, therefore, that when the steppe vegetation in Middle and Eastern Europe developed, the influence of the Siberian flora upon it was not especially

¹ **Andrees.** *Handatlas*. 1912, K. 139. Scale 1 : 15,000,000.

² **P. Krilov.** "On the Question about the Fluctuation of the Boundary between the Forest and the Steppe Provinces (Russian)." *Travaux du Musée Botanique de l'Acad. des Sciences de Pétrograd*, 14, 82-130, 1915.

³ **H. Printz.** *The Vegetation of the Siberian-Mongolian Frontiers*, pp. 12-13 and 40. Trondhjem, 1921.

⁴ *L.c.* According to Krilov all conclusions of this kind are based on fossil finds of only two animals: the *Antilope-Sajga* (*Colus sajga*) and the Siberian marmot (*Spermophilus eversmanni*), which is quite insufficient evidence in itself alone. But the Sajga is found fossil in Western Siberia only in that area where the steppes exist to-day, and fossils of *Spermophilus eversmanni* were found only on the River Jana, in Eastern Siberia, in a locality where this animal lives still, although there are no steppes.

⁵ **A. Penck.** "Die Entwicklung Europas seit der Tertiärzeit." *Rés. scient. du congrès internat. de botanique*, pp. 12-24. Vienne, 1905.

important. It is probable, indeed, that when the flora of the Siberian steppes developed, after the desiccation of the large water basins and marshes which formerly occupied the region, it received not a few of the relatively older European steppe elements. Xerophytic plants which originated in Europe and Asia mixed there together and in the course of time penetrated far into the neighbouring countries. Doubtless several Asiatic forms penetrated far into Europe. However, the extension of the direct influence, which the Siberian steppe flora had upon the European one, seems to be often overrated. It would be erroneous to draw any conclusions, by analogy, from the distribution of higher animals, whose spreading is considerably more rapid than that of plants and is not subjected to the same rules. However, even among animals, only the most rapidly moving groups show a large percentage of Siberian migrants into Europe, and not the less rapidly moving ones. Thus according to Scharff¹, the species of mammals living in Europe at the present day have, with few exceptions, migrated to our continent from other parts of the world (chiefly from Siberia). With regard to the birds it is possible that a somewhat larger number proportionally may be of European origin. Still, the great majority are to be regarded as immigrants. The autochthones are about equal to the immigrants in the reptiles, but many of the European amphibians and the majority of the fishes have probably originated on our continent. Not a single species of land or freshwater mollusc can be quoted as having migrated to Europe from Siberia in recent geological times. A very active centre of development for land mollusca lay in South-Eastern Europe, either in the Caucasus or in the Balkan Peninsula, or more probably in both. It cannot be supposed that the steppe plants were distributed in the same way as the rapidly moving higher animals, and it seems more probable that their spreading occurred in a slower way and during a longer period of time. However, even in the case of mammals, according to Scharff², it would be difficult to trace a limit between the Siberian and Oriental migrants, whose spreading took place across Asia Minor and may be much older than the direct migration from Siberia.

It would be no less of a mistake to consider the present centre of distribution of plant species as necessarily indicating the centre of their origin. Briquet³ showed, and illustrated with examples, how inaccurate it would be to confound these two entirely different facts. With even greater emphasis the same may be said concerning the distribution and the origin of steppe plants, the conditions now being much less favourable for their spreading in Europe than in Asia. N. Printz⁴ concluded as a result of his own investigations, that the steppes are spreading now in Western Siberia by natural means as a consequence of geological changes, which are occurring in Central Asia. This opinion finds a confirmation in the observations of Krilov and of several

¹ R. F. Scharff. *The History of the European Fauna*, pp. 189, 193, 196. London, 1899.

² *L.c.* p. 245.

³ *L.c.* p. 133.

⁴ *L.c.* pp. 64-67.

investigators of Central Asia, such as Huntington¹, Paulsen², etc. Krilov³ proves that the steppes in Western Siberia have been constantly spreading since the Glacial period at the expense of forests and that they have never been distributed there more widely than they are now. According to these statements the steppe vegetation in Western Siberia is still advancing towards a larger development, while in Europe its maximal development was in past geological times and the present climatical conditions are less favourable to it. In such circumstances it is not impossible that even certain xerothermic species which originated in Europe are now distributed in Asia more widely than in Europe itself.

On the contrary, there are reasons for thinking that the European flora has had sources for the development of its steppe vegetation in its close neighbourhood, namely in the Mediterranean province. According to Hagen, the xerothermic element in this province is very old. There is geological evidence that at least three centres with a dry climate and a xerophytic vegetation existed in the Mediterranean as early as the Miocene times. One of them lay in the plateau of Iran; the second in N. Africa, in the district of the Moroccan Atlas; and the third in Spain, in Mezetta and the district of Ebro⁴. During the Pleistocene the climate of the Mediterranean became moister and the above mentioned xerophytic centres disappeared. There is no doubt, however, that a certain number of xerothermic species were preserved during those unfavourable times, by their growing in some limited localities under more suitable physical conditions, just as they now exist in countries with an oceanic climate. Dry and especially limestone rocks, sandy soils, and soils rich in inorganic salts might often have been places of refuge for this type of plant. Thus may be explained, with considerable probability, the often observed attachment of steppe plants to calcareous soil, which has been noted in Germany by Drude⁵, in Sweden by Sterner⁶, etc. Velenovsky⁷ observed the same relationship in Bulgaria, and this was afterwards confirmed by other observers. Korzinsky⁸, Krasnov⁹, Tanfiliev¹⁰ found the same dependence in the

¹ E. Huntington. *The Pulse of Asia*. Boston and New York, 1907.

² L.c.

³ L.c.

⁴ H. B. Hagen. "Geographische Studien über die floristischen Beziehungen des Mediterranen und Orientalischen Gebietes in Afrika, Asien und Amerika." *Mitt. d. Geogr. Ges. in München*, 9, 144-151, 1914.

⁵ E. Drude. *Handbuch der Pflanzengeographie*, p. 382. Stuttgart, 1820.

⁶ R. Sterner. "The Continental Element in the Flora of South Sweden." *Geografiska Annaler*, 321-322, 1922.

⁷ J. Velenovsky. *Flora bulgarica. Suppl.* 1, 327, 1898.

⁸ S. Korzinsky. "The Northern Limit of the Black-earth-Steppe Province" (Russian). *Trudy Obshtestva Estestvoispyt-pri Imp. Kazanskom Universite*, 18, 214-217.

⁹ A. Krasnov. "Steppes de la Russie méridionale." *Annales de géographie*, 111, 307-309, 1894.

¹⁰ G. Tanfiliev. "Die Südrussischen Steppen." *Rés. Sc. Congrès internat. de bot.* pp. 385-387. Vienne, 1905. *Phytogeographical Investigations in the Steppe Tract of Land* (Russian). St Petersburg, 1898.

South-Russian steppes themselves, and Androsovosky¹ in the steppes of Asia Minor. This phenomenon may be explained to a certain extent on the basis that the steppe plants have retained some of their older edaphic preferences.

The richly saline bottoms of dried-up sea basins, which existed in different times and in different parts of Europe, have doubtless also been places of refuge for several halophytes with xerophytic structure. Examples are well known of halophytes, inhabitants of the sea shores, growing far in the interior of the continents. Thus *Suaeda maritima*, *Salicornia herbacea* and other inhabitants of the European sea shores may occur as far in the interior of Asia as the Abakanskaia steppe in Siberia, etc.

The steppe vegetation probably formed gradually and changed its composition in the course of time, corresponding to the changes of the climate and the salt content of the soil. In its earlier stages the soil of present South Russia and Hungary, being bottoms of former seas, was certainly rich in inorganic salts. It seems, however, that no direct connection existed at that time between Europe and Central Asia, because the characteristic representatives of the saline steppes and deserts of Turkestan are almost completely lacking in the Hungarian and the largest part of the South Russian steppes.

During all the stages of the development of the European steppe flora a direct immigration from the Mediterranean and its neighbouring countries may be more easily imagined than the often supposed migration in large numbers from the foot of the Altai, along a kind of relatively narrow corridor in Western Siberia. We have no ground for believing that the Altai itself had an especially great importance as a centre of development for the steppe vegetation. According to Krasnov² geological and phytopalaeontological data witness that a wet climate existed there during the Tertiary. It is possible that a certain number of steppe plants developed afterwards on dry rocks of the southern slopes and closed valleys of Altai, as Krasnov supposes. It can, however, be hardly supposed that the plants thus originating were of greater importance for the steppe vegetation of Europe than those originating in the same way during the dry period in the mountains of Europe itself and in its neighbourhood, such as the South Urals, Caucasus, the mountains of the Balkan Peninsula, of Middle Europe, etc. Doubtless many xerophytes originated in the interior of Asia and penetrated into Europe through the Uralo-Caspian gate. However, among all the ways which lead from the interior of Asia to Europe, this one could be used only for the relatively shortest time, which reduces its importance. Typical representatives of the Turkestan flora could spread in large numbers only as far as the Volga³.

¹ T. Androsovosky. "Vorläufiger Bericht über die im Jahre 1911 in den Steppen Kleinasien ausgeführte Reise." *Botanikay Kozlemenyyk*, **11**, 16-21, Suppl., 1912.

² A. Krasnov. "Notices sur la végétation de l'Altai." *Scripta botan. Norti Univ. Petrop.* **1**, 183-214, 1886.

³ A. Beketoff. "Sur la flore du gouvernement de Yekaterinoslav." *Scripta botan.* **1**, 32, 1886.

Xerothermic plants doubtlessly existed in many localities around the Mediterranean and especially in the neighbourhood of the old xerophytic centres, i.e. of Iran and the Iberian peninsula. From there they could easily find their way to the European steppes. These ways of distribution may be traced in several cases. Thus according to Briquet, the xerothermic plant element in the Western Alps came from Piedmont¹. From the works of Beck² and Hayek³ the influence which the flora of the Karst exercised upon the Pannonian steppe vegetation is known.

Many xerothermic plants undoubtedly immigrated into South-East Europe from Iran and Asia Minor either along the western shores of the Caspian Sea or along the western shores of the Black Sea. The researches of Medwedew, and especially his very instructive map of the Caucasus⁴, show us the route of the migration through that country. The steppe vegetation in Eastern Cis-Caucasia is directly related, according to him, to the vegetation of the dry districts of Transcaucasia. This vegetation spreads far into the interior of Transcaucasia along the valleys of Kura and Arax; it reaches the foot of Ararat and Erivan in the Armenian plateau. This vegetation is also closely related to the steppe formations of Asia Minor and Armenia⁵. On the contrary, the steppe vegetation of Western Cis-Caucasia does not show the same close relationship to Transcaucasia and Iran. These facts are easily understood, because between the two districts lies a barrier, in the shape of the moist and forested South-Euxinian zone (in the sense of Engler), which occupies the western part of Transcaucasia and the north-eastern shore of Asia Minor and which represents remnants of a thermophilous Tertiary vegetation.

No similar barrier exists west of the Black Sea, i.e. in the eastern part of the Balkan Peninsula. There are neither high mountains nor large spaces with moist climate, only a small one in the district of Strandja, which is the last outpost of the South-Euxinian vegetation. Besides this, the communication between Europe and Asia through the Balkan Peninsula is older than that across the Caucasus. In past geological times a broad connection existed between the Balkan Peninsula and Asia Minor, across the Archipelago, whereby a mass migration of plants was possible. According to C. and E. Reid⁶, whose opinion is based on phytopalaeontological data, a large number of species among the present temperate vegetation of Europe immigrated by this way from Asia

¹ *L.c.* pp. 172-173.

² **G. Beck von Mannagetta**. "Über die Bedeutung der Karstflora in der Entwicklung der Flora der Ostalpen." *Rés. scient. congrès bot.* pp. 174-178. Vienne, 1905.

³ **A. Hayek**. "Pontische und pannonische Flora." *Oesterr. bot. Zeitschr.* pp. 231-235, 1923.

⁴ **J. Medwedew**. "Über die pflanzengeographischen Gebiete des Caucasus." *Moniteur du Jardin Botanique de Tiflis*, Livr. 8, 1-66, 1907.

⁵ *L.c.* p. 46.

⁶ **C. and E. Reid**. *The Pliocene Flora of the Dutch-Prussian Borders*, pp. 22-23. The Hague, 1915. **E. Reid**. "Recherches sur quelques graines pliocènes du Pont-de-Gail." *Bull. Soc. Géol. de France*, 20, 52-57, 1920.

during the second half of the Tertiary. Xerothermic plants could also reach Europe through this immigration. There is geological evidence that centres with dry climate existed during a part of the Tertiary both in Iran and also in Central Asia¹. The existence of an extremely large number of endemics in the xerophytic vegetation of Turkestan, with many endemic genera and several monotypes among them, speaks in favour of this opinion².

Zoogeographical data also affirm the existence in the past of a large Oriental immigration into Europe. It is characteristic that this immigration is especially well expressed in those groups of animals which are biologically attached to definite plant species, and can therefore migrate only together with them. Such is the case of butterflies. A large number among them are supposed to have originated in South-West Asia, as for example the genera *Papilio*, *Thais*, *Parnassius*, *Colius*, *Danaja*, etc.

In all cases, when the vegetation of a certain country has not been previously completely destroyed by some phenomenon, like extensive glaciation, it is always most probable to suppose that the migration of plants between that country and a neighbouring one occurred in both directions, that is to say consisted in an exchange of plants between the two countries. Such an exchange probably took place between Europe and Asia in Pre-glacial times. Thus in the flora of Turkestan, genera are represented whose chief distribution and apparent place of origin lie in the Mediterranean province. In this way the vegetation of the Mediterranean and that of the Asiatic Steppe province mixed together so closely, that now they can hardly be distinguished from each other by phytogeographers. Thus may also be explained why many xerothermic plants could afterwards spread, in a relatively short time, through the steppes of Europe and Siberia and be represented in both by parallel forms (as, for example, the sect. *Pulsatilla* of the genus *Anemone*³). The Oriental immigration doubtless had a great influence upon the xerothermic vegetation of Bulgaria. Among 226 Bulgarian plants, which Velenovsky⁴ listed as having originated in Asia Minor and Armenia, a large number are xerothermic species. The route of the Oriental immigrants may be clearly observed in the vegetation of Bulgaria and the neighbouring countries. Some of them have only reached as far as the European shore of the Marmara sea, Bosphorus or Dardanelles, as for example *Silene chloraefolia*, *Dianthus lydus*, *Astragalus anatolicus*, *A. trojanus*, *Gonocyttis angulatus*, *Hedysarum varium*, *Onobrychis cana*: others reached the foot of the Rhodope,

¹ J. and C. Gregory. "The Geology and Physical Geography of Chinese Tibet." *Philos. Trans. of the Royal Soc. of London*, pp. 257-258, 1925.

² B. Fedchenko. *The Vegetation of Turkestan* (Russian). Petrograd, 1915. More than 35 endemic genera, among which more than 20 are monotypic. About 50 genera have distributional areas both in Turkestan and the East Mediterranean (in the sense of Engler).

³ Numerous closely related species are widely spread in Europe, the Orient and Asia. (Cf. A. Hayek. "Kritische Übersicht über die Anemone-Arten der Section *Campanularia* Endl." *Festschr. zur Feier des siebz. Geburtstages P. Ascherson*, pp. 451-475. Leipzig, 1904.

⁴ *L.c.* pp. 311-314.

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thus *Aristolochia hirta*, *Rhazia orientalis*, *Genista anatolica*. Several species stopped in their migration towards the north at the foot of the Balkan range, thus *Aethionema buzbaumii*, *Cleome aurea*, *Polygala rhodopea*, *Centaurea monacantha*, the spinescent representatives of the genus *Astragalus*, sect. *Tragacantha*, etc. Many other species doubtless spread farther north along this route and reached South Russia. Thus of the abundant Oriental species of the genus *Celsia* four reached Bulgaria, but only one of them penetrated as far as South Russia. The genus *Verbascum*, after its immigration into the Balkans, received here a new development and is represented now in the Bulgarian flora by more than 30 species, mostly xerothermic plants. Of the eight species of *Verbascum*, which Krasnov records for the South-Russian steppes, six are found also in Bulgaria and the other two grow in the Caucasus and Armenia.

The above mentioned *Jurinea tzar-ferdinandi*, which occurs in Bulgaria and has the character of a relict plant, connects the South-Russian *Jurinea stoechadifolia*, belonging to the Sect. *Linearifoliae*, with the representatives of the Asiatic Sect. *Stoeckmanniae*. Many more such examples could be quoted.

Corresponding to the geographical situation of Bulgaria, which lies at the boundary of the Mediterranean province, the influence of the Mediterranean flora is especially strong among xerothermic plants. A very large number among these plants belong to the Mediterranean vegetation. On the contrary, species which may be supposed to have immigrated into Bulgaria direct from Siberia, through the Uralo-Caspian gate and South Russia, are very few, even among plants commonly regarded as forming a steppe element. From this point of view interesting results may be obtained by examining a list of Bulgarian "steppe plants." Considering that the conception of "steppe plants" is not a very definite one and in order to avoid making an arbitrary choice, we shall examine only that group of Bulgarian plants, which Krasnov listed, among others, as characteristic representatives of the South-Russian steppe vegetation. Firstly it must be noted that the above mentioned species grow in Bulgaria under very various ecological conditions. Thus we meet among them several inhabitants of meadows such as *Thalictrum minus*, *Clematis integrifolia*, *Trifolium montanum*, *Polygala vulgaris*, *Orobis albus*, or even of swampy meadows, such as *Leucojum aestivum*. Others among them are representatives of the forest vegetation, as for example *Myosotis silvatica*. Many of them grow on rocks, thus *Dictamnus fraxinella*, *Silene longiflora*, *Cotoneaster vulgaris*, *Convolvulus cantabricus*, etc. Several are ruderal or half-ruderal plants, as for example *Eryngium campestre*, *Tordylium maximum*, *Inula salicina*, *I. hirta*. Chiefly on sand and rocks of the sea shore may be found *Helichrysum arenarium*, *Artemisia maritima*, *Ephedra vulgaris*. Also predominantly in the warmest parts of the country grow *Ceratocephalus orthoceras*, *Linum flavum*, *L. hirsutum*, *L. tenuiflorum*, *Haplophyllum suaveolens*,

Salvia aethiopis, etc. Others among them are on the contrary representatives of the subalpine belt of vegetation in high mountains, thus *Libanotis montana*, *Antennaria dioica*, *Sanguisorba officinalis*. Especially on subalpine and alpine rocks grows *Scutellaria alpina* (1700–2500 metres above the sea). The ecological history of the steppe vegetation has perchance left its traces in this various distribution of steppe elements.

Another interesting result may be obtained if we divide these plants both according to their geographical distribution and systematic relationship. In this way an approximate conclusion concerning their origin may be reached. Thus firstly we find a group of species which may be supposed to have grown in Europe even in Pre-glacial times. Such is a group of plants which have a circumpolar distribution or a very large distributional area in the warm belt:

Ranunculus acris	Myosotis silvatica	Festuca ovina
Turritis glabra	Euphrasia officinalis	Koeleria cristata
Antennaria dioica	Plantago media	Tragus racemosus*
Achillea millefolium	Andropogon ischaemum*	Hierochloa odorata

* Widely spread through the warm temperate and tropical zones of both hemispheres.

In the Pre-glacial strata in Europe were found:

Sanguisorba officinalis	Cotoneaster vulgaris	Thymus serpyllum
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An old origin or an old immigration into Europe may be supposed also for a group of plants which have a large area both in Europe and Asia and also systematically related forms in both continents and often also in America. To this group belong: *Thalictrum minus* (a large distributional area; found in the lower Glacial strata in Europe), *Anemone silvestris* (a large distributional area; and related forms both in Europe and Asia), *Dictamnus fraxinella* (a monotypic genus with a very large distributional area), *Vicia tenuifolia* (a large distributional area and relations in Europe and Asia); *Filipendula hexapetala* (a large distributional area; the only closely related species, *F. ulmaria*, is found in Pre-glacial strata in Europe); *Fragaria collina*, *Bupleurum falcatum* (a large distributional area; related forms in Europe, Asia and South Africa); *Turgenia latifolia* (a monotypic subgenus, widely spread in Europe and Asia through the Orient); *Antirrhinum orontium* (a monotypic section, covering a large area in Europe, Asia and N. Africa); *Ajuga genevensis* (a large distributional area; related forms both in Europe and Asia; the closely related *A. reptans* is found in Pre-glacial strata in Europe), *Ephedra vulgaris*, *Pulsatilla vulgaris*, *P. patens*, *P. pratensis*.

Especially large is the number of species, which have both their distributional area and chief relatives in the Mediterranean province (in the large sense) or in its close neighbourhood. As such may be listed:

Ranunculus illyricus	Helianthemum oelandicum	D. trifasciculatus
Erysimum odoratum	Polygala major	D. atrorubens
E. cuspidatum	P. vulgaris	D. carthusianorum
Alyssum argenteum	P. comosa	D. campestris
A. calycinum	Dianthus armeria	Gypsophila glomerata
A. tortuosum	D. pseudarmeria	Silene compacta
Camelina microcarpa	D. capitatus	S. longiflora

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<i>Alsine tenuifolia</i>	<i>A. tyraica</i>	<i>Verbascum lychnitis</i>
<i>Linum flavum</i>	<i>Galium mollugo</i>	<i>V. phoeniceum</i>
<i>L. tauricum</i>	<i>Valeriana tuberosa</i>	<i>V. blattaria</i>
<i>L. nervosum</i>	<i>Cephalaria transsilvanica</i>	<i>Veronica austriaca</i>
<i>L. austriacum</i>	<i>Inula ensifolia</i>	<i>Odontites rubra</i>
<i>L. hirsutum</i>	<i>I. squarrosa</i>	<i>Pedicularis comosa</i>
<i>L. tenuifolium</i>	<i>Echinops sphaerocephalus</i>	<i>P. campestris</i>
<i>Haplophyllum suaveolens</i>	<i>E. ritro</i>	<i>Salvia aethiopis</i>
<i>Rhus cotinus</i>	<i>E. exaltatus</i>	<i>S. austriaca</i>
<i>Genista tinctoria</i>	<i>Xeranthemum annuum</i>	<i>S. nutans</i>
<i>Cytisus capitatus</i>	<i>Centaurea solstitialis</i>	<i>S. pendula</i>
<i>C. austriacus</i>	<i>C. marschalliana</i>	<i>S. verticillata</i>
<i>Anthyllis vulneraria</i>	<i>C. scabiosa</i>	<i>Teucrium polium</i>
<i>Glycyrrhiza echinata</i>	<i>C. montana</i>	<i>Stachys recta</i>
<i>Astragalus ponticus</i>	<i>C. orientalis</i>	<i>S. angustifolia</i>
<i>A. dasyanthus</i>	<i>C. salonitana</i>	<i>Ajuga laxmannii</i>
<i>Coronilla varia</i>	<i>C. ovina</i> *	<i>Euphorbia nicaensis</i>
<i>Onobrychis gracilis</i>	<i>C. diffusa</i>	<i>E. agraria</i>
<i>Orobis albus</i>	<i>Scorzonera mollis</i>	<i>Crocus biflorus</i>
<i>O. canescens</i>	<i>Taraxacum serotinum</i>	<i>C. speciosus</i>
<i>Doryenium herbaceum</i>	<i>Lagoseris orientalis</i>	<i>Acylops cylindrica</i>
<i>Potentilla opaca</i>	<i>Phyteuma canescens</i>	<i>Andropogon gryllus</i>
<i>P. patula</i>	<i>Campanula bononiensis</i>	<i>Anthericum liliago</i>
<i>Herniaria hirsuta</i>	<i>Vinca herbacea</i>	<i>A. ramosum</i>
<i>H. incana</i>	<i>Vincetoxicum officinale</i>	<i>Allium moschatum</i>
<i>Bupleurum rotundifolium</i>	<i>Anchusa barleri</i>	<i>A. flavum</i>
<i>Pimpinella tragium</i>	<i>A. stylosa</i>	<i>Muscari racemosum</i>
<i>Seseli tortuosum</i>	<i>Nonnea pulla</i>	<i>M. botryoides</i>
<i>Tordylium maximum</i>	<i>Echium rubrum</i>	<i>Hyacinthus leucophaeus</i>
<i>Peucedanum ruthenicum</i>	<i>Onosma echioides</i>	<i>Ornithogalum nutans</i>
<i>Asperula cynanchica</i>	<i>Convolvulus cantabrieus</i>	<i>O. umbellatum</i>
<i>A. tinctoria</i>	<i>Verbascum speciosum</i>	<i>O. fimbriatum</i>
<i>A. glauca</i>	<i>V. phlomoides</i>	<i>O. tenuifolium</i>

* In Bulgaria represented by a form.

The following species are distributed both throughout the Mediterranean Region and also far into the interior of Asia. Their chief relations are, however, in the Mediterranean province, wherefore their origin is most probably a Mediterranean one:

<i>Ceratocephalus orthoceras</i>	<i>Falcaria rivini</i>	<i>C. rapunculus</i>
<i>Ranunculus oxyspermus</i>	<i>Trinia kitaibelii</i>	<i>Statice tatarica</i>
<i>Sisymbrium strictissimum</i>	<i>Galium verum</i>	<i>S. latifolia</i>
<i>Erysimum repandum</i>	<i>Knautia arvensis</i>	<i>Echinosperrum patulum</i>
<i>Alyssum campestre</i>	<i>Scabiosa ochroleuca</i>	<i>Rindera umbellata</i>
<i>Isatis tinctoria</i>	<i>Aster amellus</i>	<i>Verbascum nigrum</i>
<i>Helianthemum vulgare</i>	<i>Inula salicina</i> ¹	<i>Linaria genistaeifolia</i>
<i>Tunica prolifera</i>	<i>I. hirta</i> ¹	<i>Veronica teucrium</i> ²
<i>Silene conica</i>	<i>I. oculus christi</i> ¹	<i>V. spicata</i> ²
<i>S. viscosa</i>	<i>Helichrysum arenarium</i>	<i>V. spuria</i> ²
<i>S. supina</i>	<i>Achillea setacea</i>	<i>Origanum vulgare</i>
<i>Hypericum elegans</i>	<i>Pyrethrum corymbosum</i>	<i>Salvia silvestris</i>
<i>Lavatera thuringiaca</i>	<i>P. millefoliatum</i>	<i>Nepeta pannonica</i>
<i>Linum perenne</i>	<i>Artemisia maritima</i>	<i>N. ucranica</i>
<i>Medicago falcata</i>	<i>A. pontica</i>	<i>Scutellaria alpina</i>
<i>Trifolium montanum</i>	<i>A. austriaca</i>	<i>Teucrium chamaedrys</i>
<i>T. alpestre</i>	<i>Senecio jacobea</i>	<i>Sideritis montana</i>
<i>Astragalus cicer</i>	<i>S. erucifolia</i>	<i>Euphorbia gerardiana</i>
<i>A. onobrychis</i>	<i>S. doria</i>	<i>Poa bulbosa</i>
<i>A. exscapus</i>	<i>Jurinea arachnoidea</i>	<i>Iris pumila</i>
<i>A. vesicarius</i>	<i>Tragopogon major</i>	<i>Asparagus officinalis</i>
<i>A. albicaulis</i>	<i>T. orientalis</i>	<i>Allium verticillatum</i>
<i>Lathyrus tuberosus</i>	<i>T. brevisrostris</i>	<i>Ornithogalum narbonense</i>
<i>Sanguisorba minor</i>	<i>Campanula sibirica</i> (Caucasian or Iranian origin)	<i>Gagea pusilla</i>
<i>Eryngium campestre</i>		<i>Thesium ramosum</i>

¹ Cf. **G. Beck**. "Inulae europaeae." *Denkschr. Akad. Wiss. Wien*, **44**, 1881.

² According to **E. Wulf**. *Crimo-Caucasian species of the Genus Veronica* (Russian), 1915.

Another group of species is widely spread through the Mediterranean (the Orient) and the interior of Asia; their relations lie in Asia or are vague. This group represents most probably the Oriental immigration. To this group belong:

<i>Adonis vernalis</i> *	<i>Artemisia campestris</i>	<i>Stipa capillata</i>
<i>Erysimum canescens</i>	<i>A. scoparia</i>	<i>S. pennata</i>
<i>Gypsophila paniculata</i>	<i>Chondrilla juncea</i>	<i>Triticum cristatum</i>
<i>Glycyrrhiza glabra</i>	<i>Androsace maxima</i>	<i>Linosyris vulgaris</i>
<i>Astragalus austriacus</i>	<i>A. elongata</i>	<i>L. villosa</i>
<i>Spiraea crenifolia</i>	<i>Phlomis tuberosa</i>	<i>Kochia prostrata</i>
<i>Libanotis montana</i>	<i>Euphorbia virgata</i>	

* The immigration route is not completely clear; it may have been the Siberian one, but more probably was across the Caucasus.

Some of them may have immigrated into Europe through the Caucasus. *Kochia prostrata* may as likely be of European as of Asiatic origin; its spreading, however, occurred probably through the Orient.

The following species have their distributional area and relationship chiefly in Europe, yet not in its Mediterranean part: *Ranunculus polyanthemos*, *Hesperis tristis* (Pontic distribution and relations), *Viola hirta*, *Arenaria rigida* (Pontic distribution, relations in the Mediterranean province and in Asia), *Geranium columbinum*, *Potentilla recta* (Pontic origin, according to T. Wolf¹), *P. inclinata*, *P. argentea*, *Peucedanum alsaticum*, *Serratula heterophylla*, *S. tinctoria*.

The following species are spread through Eastern Europe and Siberia, but are lacking in the Orient; their distribution may be supposed to be the result of a direct exchange between Europe and Siberia through the Uralo-Caspian gate: *Paeonia tenuifolia* (the origin is not quite clear, it may be South Uralian, North Caucasian or West Siberian); *Silene chlorantha* (most probably of European origin but spread far towards the east); *Caragana frutescens* and *Astragalus testiculatus* are of Asiatic origin and their immigration into Europe occurred probably directly from Siberia, although possibly through the Caucasus. *Amygdalus nana*, *Prunus chamaecerasus* and *Adenophora liliifolia* may be considered as direct immigrants from Siberia.

Thus among the named steppe element in Bulgaria the number of species which may be supposed to be direct immigrants from Siberia is very insignificant, especially in comparison with the number of species which have probably originated in the Mediterranean province (in a broad sense). It must be emphasized, however, that the above analysis and its results cannot claim to have an absolute value. Neither the geographical distribution nor the present taxonomic relationship by itself is able to show with certainty the place of origin of a species. The inexactness of both methods of investigation has been proved by Kerner² and Briquet. By neither method can more than a certain probability be reached. Therefore on the basis of the above analysis

¹ "Monogr. d. Gatt. *Potentilla*." *Bibliotheca Botanica*, N. F. 1, 1908.

² *Pflanzenleben*, II. 838, 1891.

only one general conclusion can certainly be reached, that the so-called "steppe plants" in Bulgaria are chiefly of Mediterranean origin.

Considering the geographical situation of Bulgaria this result is very natural, especially if we remember that even in the South-Russian steppes of the government Yekaterinoslav, Beketoff found a larger number of Oriental (Caucasian) immigrants than of plants which had migrated direct from Turkestan and Siberia¹.

From the circumstance that among plants common to Bulgaria and the South-Russian steppes the Mediterranean elements prevail, it is evident that the migration of plants between the two countries occurred chiefly in the direction from south towards north, and to much less extent in the opposite direction. This migration occurred probably as the climate was gradually becoming warmer after Glacial times and as a result of the climatic changes.

¹ *L.c.* pp. 75-78.

SOIL SOURNESS AND SOIL ACIDITY

By W. H. PEARSALL.

(With one Figure in the Text.)

In a recent number of this JOURNAL (14) criticisms have been directed at a suggestion put forward by the writer in 1922 to explain some cases of soil sourness (11). Since these criticisms appear to be founded upon a misconception and mis-statement of the original suggestion it is necessary to refer to them in some detail and the opportunity may also serve to draw attention to some of the problems facing the student of the subject.

The majority of investigators fail to distinguish *soil sourness* from *soil acidity* (or the hydrogen ion concentration of the soil). These two factors are usually associated in nature but they are not of necessity the same nor even interdependent. There are, of course, a number of factors which also are often or usually found in soils which are sour, e.g. deficient nitrification, deficient aeration, high organic content, organic soil toxins. It is advisable to keep all of these factors in mind in discussing the phenomenon of soil sourness for any of them may serve to prevent the growth of normal plants on sour soil. The heathy plants which are found on sour soils in nature are clearly able to withstand all the factors which normally occur in such soils and it appears to be true that these plants are also "calcifuge" and unable to grow on normal soils. The problem thus assumes great complexity. We have not only (i) to determine the factors which prevent normal plants from growing on sour soils but we have also (ii) to find an answer to the question why heathy species *can* grow on sour soils, but (iii) cannot grow on normal soils. These three groups of problems *may* be different aspects of the same problem. The present evidence, however, suggests that they are not.

Turning now to the soil side of the problem, we have first to recognise that soils may apparently be *sour* and yet only slightly or not at all *acid*. This is another aspect of the fact, to be considered in detail below, that the distribution curves of species in relation to the hydrogen ion concentration, overlap enormously. We may thus find heathy species growing profusely on soils whose pH value lies between 6 and 7. In order to explain cases of this kind the writer suggested in 1922 that soil sourness might be attributed (*a*) to calcium deficiency in the soil and (*b*) to a high proportion of potassium and sodium to calcium (and magnesium). This suggestion was based on the examination of the waters of some nearly neutral gravels on which *Calluna* and *Nardus* were growing, together with the known fact that calcium leaches

from normal colloidal soils more rapidly than potassium and sodium. Leaching is one of the principal causes of soil sourness and it clearly leads to an increase in the $\frac{K + Na}{Ca}$ ratio in the soil (11). The problem is capable of being attacked from another angle. If heathy plants can only grow on soils deficient in calcium then the basic ratio *must* be of fundamental importance to them, because the physiological effects of calcium can be "antagonised" or removed by potassium and sodium. The literature is full of instances of this fact and we may be pardoned for not taking specific cases in detail. The position of magnesium in regard to these physiological activities is intermediate. It "antagonises" both potassium and sodium, and also calcium. Since, however, the principal factor in determining the basic ratio in soils is calcium deficiency, the behaviour of magnesium is, at the moment, of small importance except in those soils where it is present in predominant quantities.

Dr Salisbury (14) has recently subjected the suggestion outlined above to some detailed criticism, although the value of his criticisms is considerably lessened by the fact that he has not even stated the basic ratio hypothesis correctly, for he describes it as the "ratio between *calcium and sodium* and *potassium and magnesium*." (The italics are his.)

His criticisms are (1) that the chemical composition of the soil solution cannot be inferred from soil analyses, and that the proportions of potassium extractable from soils are subject to great variations in relation to the water content of the soil; (2) that the basic ratio hypothesis involves the assumption that plants of calcareous soils are intolerant of high potassium contents and that the Rothamsted manurial experiments indicate that soil acidity is lessened by the addition of potassium salts; (3) that Masall's results indicate that the growth of wheat in water cultures is related to hydrogen ion concentration rather than to the basic ratio.

The impartial critic would doubtless agree that all of these arguments are irrelevant so far as the published statements of the basic ratio hypothesis are concerned. Nevertheless we will consider these points in detail.

1. If the composition of the soil solution cannot be inferred from soil analyses, then we cannot use such data to argue for or against the hypothesis under consideration. This hypothesis was not, however, based primarily on soil analyses, but (a) on analyses of water washed through gravel or flowing through it; (b) on the known facts of leaching and base exchange in normal soils. Further, one cannot imply, as does Dr Salisbury, because it is difficult to obtain information about the soil solution, that the composition of this solution has little or no effect upon the plants growing in it.

The only grounds on which we can infer the possible composition of the soil solution, namely, from the expressed soil waters, from drainage waters, water extracts, acid extracts, and salt extracts, all alike indicate that the calcium content of the soil is subject to great variation in different soils and

is lowest in sour and acid soils. In regard to the basic ratio, our information is limited since analysts do not usually estimate all the soil bases. By the salt extraction method, Kelley and Brown (8) have shown that the replaceable bases of acid soils possess a basic ratio averaging about twice that of normal soils, although their results exclude the calcium carbonate present, and hence give a much higher basic ratio for the normal soils than would really exist. Olsen's figures (9), which are summarised below, refer to extracts with water saturated with carbon dioxide, but they similarly indicate a higher basic ratio for acid soils.

	No. of soil					
	6	14	7	18	20	19
pH value	4.9	4.9	6.1	6.2	6.2	7.3
K + Na	0.95	1.13	0.25	0.20	0.14	0.16
Ca + Mg						
K + Na	1.32	1.30	0.27	0.21	0.14	0.19
Ca						

Olsen (9, 10) also supplies larger numbers of partial analyses giving only the potassium and calcium contents of the carbonated water extracts. These also show that a higher K/Ca ratio occurs in such extracts from acid soils, and there is a certain amount of variation in the ratio for slightly acid soils, so that we have clearly to keep acidity and the basic ratio distinct as soil factors. They are not exactly proportional.

Dr Salisbury's criticism that the amount of potassium extractable from soils is subject to great variation in relation to the soil water content, does not appear to me to be of much value. Some of the most important soil properties may be subject to great variation, as, for example, its water content and nitrate content. But Dr Salisbury makes the astonishing statement that these fluctuations are shown in "determinations based on the actual soil solution." This statement is incorrect, since the fluctuations are obtained by comparing the expressed soil solutions, from soils containing *at most* 23 per cent. of water, with the water extracts (one part soil to five water) which represent a "water content" of 500 per cent. (Burgess, 3). It is not justifiable on these data alone to infer that the potassium content of the soil solution from any single soil is subject to great variations under natural conditions, especially since in the figures given by Burgess there is no relation between the amount of soil moisture and the potassium content of the soil solution for the different soils examined. The whole argument, however, is irrelevant. If we are to consider the basic ratio hypothesis, then we require to compare the calcium content of the soil solution and its basic ratio. The data given by Burgess (3) indicate, as far as their completeness and analytical precision will allow, that the two factors we require fluctuate in the same directions in the water extract as they do in the soil solution. The soils with the highest basic ratios in the water extracts are those with the highest basic ratios in the expressed solutions.

2. The basic ratio hypothesis does not necessarily involve the assumption that the plants of calcareous soils are intolerant of high proportions of potassium. It does not refer to such soils or to such plants (11) and it was, in fact, expressly stated in such a form as to refer only to soils poor in calcium. There are obvious reasons for this. At least two classes of soils exist which may be relatively rich in calcium salts and which have also a high basic ratio, namely, (1) salt marsh and similar marine soils, (2) "alkali" soils as found in arid regions. While the plants of these habitats may have some similar structural features to those of sour soils, we have at present no other justification for comparing them. The further criticism that the addition of potassic manures to the Rothamsted plots has not increased the acidity or sourness of these plots, is thus beside the point, since the soils used are relatively rich in calcium. Further, the addition of potassium salts to soil does not necessarily increase either the content or proportion of potassium in the soil solution. The actual result of such a treatment will vary with the nature of the treated soil. In the case of a calcium rich normal soil like that at Rothamsted, the probable result of adding potassium salts would be that the potassium would be "adsorbed" by the soil, while other bases, and *principally calcium*, would replace it in the soil solution. That some such change takes place at Rothamsted may be inferred, not only from the increase in the production of leguminous species, but also from Voelcker's analyses of the drainage waters, which show little or no change in the potassium content but a very largely increased proportion of calcium (6). It cannot be argued that this would always be the result, for if the soil were deficient in bases, iron and aluminium would be liberated on adding the potassium salt, as in Comber's test for soil sourness (5). There may also be a third case, that of acid peaty soils deficient in iron and aluminium, where the addition of neutral potassium or calcium salts may cause a decided increase in hydrogen ion concentration. The origin of this increased acidity is at present unknown.

It is necessary to enlarge on these points in order to demonstrate that one must be very cautious in arguing from manurial experiments, unless fairly precise data as to effect are available. The considerations outlined above, however, suggest a possible cause for the well-known fact that soil sourness is removed most thoroughly by lime and not by addition of any calcium salt. Remembering that soil sourness and soil acidity are usually associated, then we have probably two extreme cases to consider:

(1) The addition of lime removes both sourness and acidity.

(2) The addition of calcium salts of strong acids, e.g. chlorides, sulphates, removes calcium deficiency but *increases* acidity.

In the second of these cases, a high hydrogen concentration may still remain as a bar to the growth of normal plants, so that this treatment would not materially improve the crop-producing power of the soil.

3. Dr Salisbury accepts and refers to Masall's results that wheat shows a definite optimum growth in relation to hydrogen ion concentration but none in relation to the basic ratio of the culture medium. It may be pointed out that the basic ratio hypothesis was not devised to account for the growth of wheat, but as an explanation of the distribution of heathy plants. The fact that different species behave in very different ways is beautifully illustrated by the case of barley. This cereal is extremely sensitive to soil sourness (much more so than wheat) but less sensitive to high hydrogen ion concentrations (Olsen, **10**, Arrhenius, **2**). There are grounds for believing that high proportions of available aluminium may be the toxic element in sour soils in this instance (Olsen, **10**, Hartwell and Pember, **7**) and an analogous case is apparently that of the tea-plant (**4**).

On the other hand, Olsen (**10**) found that barley alone of the acid and alkaline soil plants he tried was sensitive to aluminium. It is, therefore, pretty clear that we cannot apply either the barley or the wheat result to other plants without further evidence. A variety of reasons have been suggested (and on good evidence) to account for the inability of normal plants to grow on sour and acid soils and individual species may well be limited to normal soils by their inability to grow well in the presence of any one of the following factors, viz. (i) high hydrogen ion concentration, (ii) low calcium content, (iii) low calcium and high proportion of aluminium and/or iron, (iv) low calcium and high basic ratio, (v) organic toxins, (vi) scarcity of available nitrogen, (vii) scarcity of oxygen. It would be folly to assert, in the present state of our knowledge, that any one of these factors kept off all normal species from sour soils. Advocates of the case for hydrogen ion concentration (Olsen, **10**, Salisbury, **14**) overlook two very important points: (i) that sour soils exist which are not or only slightly acid, (ii) that the limits of distribution in nature, and even of successful growth, occur at very similar hydrogen ion concentrations for perhaps the majority of species. For example, the distribution curves for *Pteridium aquilinum* and *Vaccinium myrtillus* (or for *Ficaria* and *Mercurialis*) given by Salisbury (**14**) show remarkable similarity and it is clearly not permissible to assume that hydrogen ion concentration exerts any appreciable rôle in differentiating their distribution in the localities examined, although possibly most ecologists would regard *Vaccinium* as the plant more characteristic of sour soils. Even when the average distribution curves show different modes, e.g. *Vaccinium myrtillus* and *Mercurialis perennis*, there is often a very considerable overlap of the pH ranges, and this may be much greater for the species mentioned than is indicated by either Olsen (**10**) or Salisbury (**14**). For instance, in the Crag Woods (N. Lancs.) *Mercurialis* grows in abundance between pH 4.9 and 6.2, while the similar values for *Vaccinium* in these woods were pH 4.2 to 6.0. We are not justified in saying that hydrogen ion concentration determines the distribution of these species in this instance. On the other hand, all the *Vaccinium* soils tested

were "sour" with Comber's thiocyanate test (5), while those under *Mercurialis* were not. It is, in this instance, reasonable to attribute soil sourness to the quantity and character of the soil bases, and this, rather than the pH value, appears to be associated with the distribution of the vegetation.

A similar overlapping of ranges of hydrogen ion concentration, which is of interest, is that shown by *Phragmites communis* compared with *Eriophorum* (either *vaginatum* or *angustifolium*). The pH ranges (not necessarily extreme for these plants) are pH 7.7-5.0 (*Phragmites*), 7.0-3.7 (*E. angustifolium*) and 6.1-3.5 (*E. vaginatum*) for localities where the species were abundant but not intermixed. These results are of interest because both *Phragmites* and *Eriophorum* are tolerant of high proportions of aluminium (Stoklasa, 16) and we seem to have here a case in which neither aluminium nor acidity can be regarded as the decisive factor over the overlapping ranges.

These instances are only a few among the many which might be cited. We can state the problem in a more general, yet equally definite way. Practically all species are able to grow abundantly on soils whose pH value lies between pH 5 and 6.5, yet some of these soils bear "sour" types of vegetation and others do not.

One other point remains to be considered. What importance are we to attach to curves showing the incidence of species in relation to the hydrogen ion concentration of the soil? Salisbury (14) appears to attach considerable importance to these curves in spite of the objections to which they are open, and his results may be taken as representative. In actual fact such curves require very careful analysis before any arguments can be based on them. The need for analysis will be apparent from the following considerations. Curves showing the incidence of a species in relation to any variable soil factor would presumably obey the general rule and show a "mode" comparable to the "mode" shown in Salisbury's curves. We require, at the very least, to know if the differences between the various modes (for different species) are significant or not. From the overlapping nature of the curves this appears to be improbable. Furthermore, no attempt is made to eliminate the influence of the curve, showing the relation of number of soils examined to the various pH classes. Olsen (10) has attempted this by expressing his results as "percentage frequencies" or as "percentages of localities examined." Presumably Salisbury's curve for *Psamma* "frequency" at Blakeney Point is of the same sort, though information on this vital point is lacking. Even so it cannot be claimed that the influence of the "soil curve" is eliminated. According to Salisbury's own data (15) about 62 per cent. of the Blakeney beach and dune soils lie between pH 6.9 and 7.2, and it is therefore extremely probable that *Psamma* will be most frequent at these pH values (see Fig. 1).

Salisbury further draws attention to what he characterises as the "bi-modal" incidence curve shown best by *Fagus*, *Mercurialis* and *Ficaria*. All of these species show modes at the same places, pH 6-6.5, and pH 7-7.5. Now

Salisbury gives no data as to the number of soils examined in each of the pH classes, so that the influence of the "soil curve" on these modes cannot be estimated. My own random collection of soil pH values (for north of England woodlands) includes a fair range of both siliceous and calcareous soils and will, perhaps, serve to indicate the effect of the number of soils occurring in each of the pH classes. Curiously enough, the data show modes at precisely the

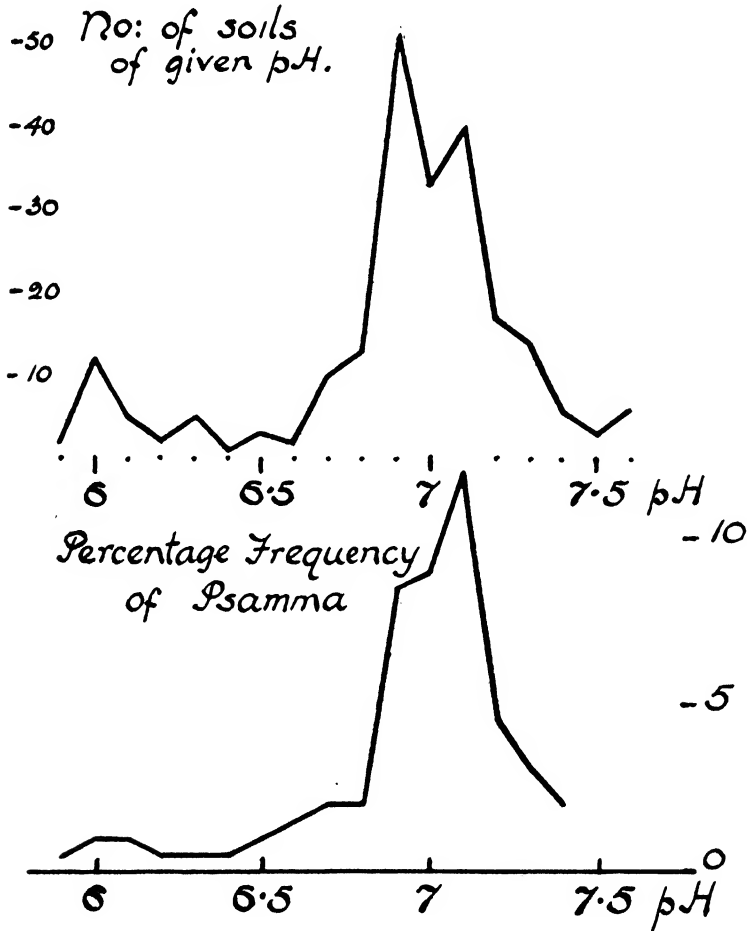


FIG. 1. The curves for "Percentage Frequency" of *Psamma* at Blakeney and the number of soils recorded by Salisbury at each pH value for the beaches and dunes at Blakeney Point.

pH values at which the modes for the incidence curves occur in the cases mentioned above:

Numbers of recorded pH values for soils of different types.

	pH class							
	4-4.4	4.5-4.9	5-5.4	5.5-5.9	6-6.4	6.5-6.9	7-7.4	7.5-8
1. Calcareous (Yorks.) ...	—	—	—	—	8	19	31	12
2. Calcareous clay (N. Lancs.)	—	2	4	9	17	14	26	4
3. Siliceous* ...	10	41	26	29	30	11	3	—
Total ...	10	43	30	38	55	44	60	16

* Carboniferous and Red Sandstones, Silurian.

The bimodal incidence curve, for the three species under discussion, is clearly suspect, especially since all of these three species occur both on calcareous and siliceous soils. Still further examination reveals other objections to the bimodal incidence curve. It is not shown in Olsen's data for either *Mercurialis* or *Ficaria* (10), and for the relatively few cases in which he obtains a bimodal curve (*Festuca* and *Taraxacum*) Olsen puts forward the suggestion that the species includes different sub-species which tend to occur at different hydrogen ion concentrations. Secondly, data from the north of England for the distribution of *Mercurialis* in relation to hydrogen ion concentration do not indicate a bimodal form. In fact the maximum number or percentage of occurrences occurs in the region (pH 6.5-6.9) given by Salisbury as the depression between two modes.

pH values of soils on which Mercurialis was abundant.

	pH class						
	4.5-4.9	5-5.4	5.5-5.9	6-6.4	6.5-6.9	7-7.4	7.5-8
No. of records...	1	5	6	8	16	9	2
% of total soils*	2.3	16.6	15.8	14.5	36.3	15.0	6.2

* Percentage of the total number of woodland soils examined in each pH class.

Thus the bimodal incidence curve cannot be regarded as a satisfactory basis for argument, until the data have received careful statistical analysis and until the present discrepancies in the evidence have been reconciled. It may further be pointed out that the comparison of these bimodal-incidence curves and the curves obtained by growing plants in culture media at different pH values is not a happy one. The growth curves *may* show a bimodal form when expressed graphically—but there is no sort of agreement between the results of different investigators or even the same investigator (1, 2), either as to the existence of a bimodal curve, or as to the points at which maxima occur.

The comparison between the incidence curves and the results obtained by Robbins (13) for the swelling curve of potato is equally unfortunate. Apart from the fact that the depression in Robbins' swelling curve occurs at a different pH value from that in the incidence curve, the most cursory examina-

tion of Robbins' data shows that he has ignored any other depressions in the swelling curve which did not occur in the region pH 5.5-6.0. Swelling curves for plant tissues in relation to different hydrogen ion concentrations are, in fact, composed of a series of "modes" and depressions. At least four depressions exist in the potato swelling curve (12), and other tissues examined are essentially similar. It is, therefore, not permissible to institute any comparisons between these curves and bimodal incidence curves.

The above analysis of the evidence may serve to draw attention to three main problems which require consideration:

- (i) *Soil acidity* appears to be distinct from *soil sourness*.
- (ii) A variety of factors may prevent normal plants from growing on sour and acid soils.
- (iii) Data grouped as "incidence" curves require detailed analysis before general conclusions can be based on them. (This would appear to be true of all such data where the distribution ranges overlap.)

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REVIEWS

TREE MYCORRHIZA

Melin, Elias. *Untersuchungen über die Bedeutung der Baummykorrhiza.* Eine ökologische-physiologische Studie. Gustav Fischer, Jena: 1925. Pp. vi + 152 and 48 figures in the text.

Melin's researches on the mycorrhiza of pine, spruce, larch, birch and aspen (Melin, 1921, 1922, 1923, 1924) marked the beginning of a new period in our knowledge of tree mycorrhiza, and already constitute a substantial contribution towards the solution of a much discussed and highly controversial aspect of the mycorrhiza problem. The indebtedness of foresters and botanists to their Swedish colleague is increased by the publication of the papers now under review, in which fresh light is thrown upon the physiology of mycorrhiza in forest trees.

Summarising his earlier work on the mycorrhizal fungi of Conifers, Melin adds the names of several Hymenomycetes to the list of those already identified experimentally as mycorrhiza-formers in pine and spruce, viz. *Amanita muscaria*, *Cortinarius muscosus*, *Lactarius deliciosus*, and *Russula fragilis* on pine; and *Amanita muscaria*, *Cortinarius balteatus*, and *Lactarius deliciosus* on spruce.

He offers also a warning on the need for caution in drawing conclusions from negative results in artificial cultures by reason of the changes known to be induced in the root-fungi under these conditions. He had shown in an earlier paper that the production of mycorrhiza in trees is determined by the physiological states of both symbionts, that of the fungus being especially prone to variation in respect to the qualities which determine "virulence." Accepting this view, the formation of mycorrhiza in Conifers is a "reciprocal phenomenon," a conclusion in agreement with that recently put forward in respect to heather (Rayner, 1924).

The greater part of the present paper is concerned with the results of a long series of experimental cultures designed to investigate the nutrition of both symbionts in Conifers-mycorrhiza and throw light upon their mutual relations.

The conclusions already reached by the author himself are clear from his earlier works. Thus: "Die Birken- und Espenmykorrhiza ist kein parasitisches Gebilde, wie es z. B. McDougall meint, sondern Pilz und Wurzel leben in mutualistischer Symbiose miteinander" (Melin, 1923, p. 517); and, again, after summarising the case for a mutual relation in pine and spruce under conditions favourable to mycorrhiza formation: "Diese optimal entwickelte Mykorrhiza ist u. a. auf gutem Rohhumus und auf zur Aufforstung dränierten Moorböden schön vertreten. Ist der Pilz hier Parasit an der Wurzel oder leben beide in mutualistischer Symbiose zusammen? Auf diese Frage gibt es nur eine Antwort: Wurzel und Pilz leben in mutualistischer Symbiose" (Melin, 1923).

Experimental evidence in support of these views has been obtained from the behaviour of the root fungi and their hosts when supplied with various nutrients and is marshalled in the paper now under consideration. It relates especially to the following aspects of the problem: (1) the general reactions shown by the two symbionts under pure culture conditions, with special reference to nitrogen assimilation; (2) the application of these experimental results to the conditions found in nature.

1. The technique adopted for growing seedlings in pure culture with and without infection was simple and effective. For synthetic cultures the use of sand watered with a suitable nutrient was preferred to humus, owing to the toxicity of sterilised humus to the mycorrhizal fungi; under experimental conditions mycorrhizae were formed only in sand cultures.

Under pure culture conditions, the root fungi of pine and spruce display great variability in growth on favourable media. Some, e.g. the species of *Boletus* associated with pine, are relatively vigorous, others make very feeble growth or are maintained with difficulty in artificial cultures.

As compared with indifferent species and casual soil fungi, they are more easily affected by changes in the substratum and are extremely sensitive to the H-ion concentration of the medium. Whereas the former grow indifferently over a wide range of pH values, the root fungi, with few exceptions, prefer an acid substratum, and are incapable of growth at pH values on the alkaline side of neutrality. Optimum conditions for the fungi of pine and fir are provided by pH values between 4.0 and 5.0. In this connection it is of interest to note that pH values about 4.0 have been recorded for the humus layers of coniferous woods throughout middle and northern Europe by Hesselman (1917), and that Brenner (1924) found pH values ranging from 3.5 to 4.8 in similar soils in Finland.

Of particular interest is the reaction shown to small amounts of phosphates by these fungi, in view of Hansteen-Cranner's (1922) observations on the giving off of these substances by the roots of the higher plants under certain conditions. In Melin's experiments, growth was markedly stimulated when the fungi were brought from pure culture into contact with seeds and seedlings of pine and spruce.

Melin was satisfied that the effect was due to excreted phosphates, and attaches great importance to these observations by reason of the special growth relations shown by the mycorrhizal fungi in nature.

The behaviour of these fungi in relation to nitrogen assimilation is of special importance. No evidence whatever was obtained that any of the forms can utilise atmospheric nitrogen; salts of ammonia, urea and nucleic acid all serve well as sources of nitrogen, while individual fungi can make use of peptone, asparagin, and a number of other organic compounds with equally good results.

A long series of experiments with various carbon compounds led to the conclusion that growth was satisfactory only when glucose was supplied, thus supporting the popular belief that mycorrhizal fungi obtain supplies of carbon from the root cells of their hosts. Direct experiments on the utilisation of the organic compounds in humus were limited by the toxicity of this material when sterilised by heat, but humus extracts freed from micro-organisms by filtering gave weak growth, and the addition of glucose produced vigorous development as on favourable soil.

The reaction of pine and spruce seedlings to various nutrients in pure culture was tested by germinating sterilised seeds, and growing the resulting seedlings in sand and humus cultures in special culture flasks for periods of two to three years. The capacity of such seedlings for independent growth had been determined in earlier experiments (Melin, 1923). Compared with uninfected seedlings they exhibit characteristic structural features in the root systems and have incidentally provided proof that there is no obligate relation with the root fungi, such as occurs in the developmental stages of orchids and heaths.

A series of experiments designed to test the reaction of these seedlings to possible sources of nitrogen led to the following conclusions. There is no fixation of free nitrogen; inorganic compounds of nitrogen, e.g. potassium nitrate and ammonium chloride, provide

suitable sources of nitrogen; simple organic compounds, e.g. asparagin, can be readily utilised; more complex compounds, such as peptone and nucleic acid, are used with difficulty, as evidenced by the excessive length of roots in cultures to which they were supplied.

Similar seedlings of pine and spruce, after inoculation by appropriate root fungi, produced typical mycorrhiza in sand culture. Experiments with various nutrients confirmed the conclusions indicated by the behaviour of fungi and seedlings when growing alone.

In view of its great importance, the possibility of nitrogen-fixation by the mycorrhiza in synthetic cultures was carefully tested and gave negative results, the small increase in nitrogen content at the close of the experiments being regarded as due to atmospheric impurities.

The reaction shown by these synthetic seedlings to various compounds of nitrogen is specially important in view of the long controversy about nutrition in mycorrhizae and their relation to the soil humus.

The comparative growth of cultures supplied respectively with ammonium chloride, peptone and nucleic acid was determined by dry weight estimations, and the figures obtained after three years' growth are supplied in Table 41 of the present paper. Evidence of the general condition of the cultures is provided by photographs of the seedlings after removal from the culture flasks, and is particularly impressive in the case of the nucleic acid cultures (pp. 82, 83). The roots of the seedlings with mycorrhiza are one-third, or less than one-third, as long as those of uninfected control seedlings, and exhibit none of the characteristic symptoms of nitrogen starvation shown by the latter.

When combined with evidence drawn from the figures supplied in the tables, these observations appear to justify Melin's main conclusion: "Diese Versuche zeigen, dass die Mykorrhizen auf komplizierteren organischen Stickstoffverbindungen, beispielsweise Nukleinsäure und Pepton, für die Pflänzchen nützliche Gebilde sind. In Reinkulturen vermitteln nämlich die Mykorrhizen den Pflänzchen die Aufnahme der erwähnten N-Verbindungen im grossen und ganzen leichter, als dies die Wurzeln allein tun kann."

2. The application of these experimental results to conditions found in nature is of particular interest in view of the controversial views expressed by earlier workers, in respect to the significance of mycorrhiza in forest trees.

Observations on the H-ion concentration most favourable to the root fungi have been supplemented by field observations, as mentioned above, and become significant when it is realised that it is only in humus soils of the more acid type that coniferous mycorrhiza is freely formed in nature. Moreover, it is in soils of this class, i.e. those consisting largely of raw humus (Rohhumusböden), that the nitrogen supply exists chiefly in the form of organic compounds of relatively complex type.

In humus soils with a more neutral reaction (Mullböden), e.g. those of heaths, coniferous mycorrhiza only appears sporadically, and it is suggested by Melin that its formation may be directly related to the known differences of behaviour in such soils in respect to the breakdown of organic material and the rate of nitrification.

With regard to the distribution of the mycorrhizal fungi in nature, great importance is attached by Melin to the supply of phosphates associated with roots. It is suggested that these substances may be indispensable to the fungi, perhaps for the production of fruit bodies, perhaps in relation to the germination of spores.

The main contention in this paper, namely, that mycorrhiza possesses a vital significance for trees and other plants growing in acid humus, if correct, opens up a whole new field for experimental enquiry, since it becomes of the first importance to provide conditions favourable to the formation and active functioning of mycorrhiza. This is especially true

in relation to forestry, since in woodland soils the amount of humus present is constantly increased by the process of leaf fall.

In a summarised account, it is not easy to do justice to the wealth of observation and experiment that have made the publication of this paper possible. Its value is greatly enhanced by the large number of tables supplied in the appendix, in which the author's experimental results are clearly set out.

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SOUTH AFRICAN PLANT FORMS

Bews, J. W. *Plant Forms and their Evolution in South Africa.* London, 1925. Pp. 199, 31 figures and 1 map.

The flora of South Africa has been long regarded as being one of very great interest from many points of view, and not least from the fact that it contains two very widely separated elements. The one, and to botanists outside, probably the better known, occupies a rather restricted area in the south-west portion; the other is much the more widespread flora and occupies the central and eastern portions.

For the study of plant migrations and the possible phylogenetic history of such floras or of any special types of plants, South Africa possesses very many advantages. The continent is a very old and stable one, and the land connection with the tropics and the northern hemisphere has remained unbroken, at any rate from the time of the evolution of the angiosperms. The climate also, although it has undergone fluctuations, has not had any of the violent devastating changes that have taken place in the north. At the present time South Africa exhibits considerable varieties of climate each with its own characteristic vegetation type.

In commencing to trace an evolutionary sequence of plant form and, hence, indirectly, of vegetation types, the author distinguishes two types of habitat. The first are those which have persisted for immense periods of time practically unchanged, what are termed primitive types of habitat. These are claimed to have remained unchanged since the evolution of flowering plants. The second are changing or derivative types of habitat which have not this long unchanged history. The former are represented by moist tropical or subtropical forest, marshes or swamps, stream sides, sea shores, and possibly mountain tops. The vegetation in all these cases is very widespread and covers very wide geographical areas without change of type. It is in these primitive habitats that the most ancient growth forms are looked for. In determining on these, use is made of confirmatory evidence from other sources, such as floral morphology, structure and so on. The most primitive forms are regarded as being represented by the tree with broad simple leaves and by the halophyte.

All other types are derivatives and have been evolved in relation to increasing aridity. Evolution of growth form is regarded as being a progression from the hygrophYTE towards the xerophyte. Extreme xerophyte desert plants, succulents, etc., represent very modern forms. The annual is regarded as the most highly evolved growth form. Certain plants, e.g. Gymnosperms, are considered on a different basis; these plants, very few in number in South Africa, are looked on as possible relics from a pre-angiosperm flora.

Accepting this scheme of evolution of growth form, the author argues that succession passes through a series of stages that are the reverse of those passed in the evolution. The succession series is utilised in the building up of the phylogenetic story of the flora: statistics of growth forms, numbers of genera and species and so on are quoted in support of the theory advanced.

These premises form the basis for the sketch of the origin and migrations of the flora. That of the east and the central region is regarded as having come from migrations of plants from the tropics and subtropics. Here a good and connected argument is advanced in support. This is the author's own ground and the account here is much more living than other portions of the book.

A special chapter is devoted to the origin and establishment of grassland which forms such an important part of the South African vegetation. It is claimed that the evolution of the grass-like plant enabled the angiosperm flora to occupy vast areas that previously it could not penetrate. The impression left with the reader, however, after reading this chapter, is that this exceedingly perplexing question has not been advanced towards solution.

The chapters on the Karroo and Deserts and on the south-west flora are much less happy than the earlier ones, and cannot be said to advance our knowledge of the flora to any appreciable extent. As regards the last, the author does not commit himself definitely to either of the prevailing views as to its status, though he inclines perhaps towards origin by mountain range migration from the north. While emphasis is laid on the penetration of eastern and Karroo genera and species into this flora, the reverse is not mentioned; but surely such a genus as *Pelargonium*, for example, with a few specialised Karroo species and a large number, often with much less highly evolved growth forms, in the south-west, might be regarded quite as fairly as showing a north-east migration. All through, however, there seems to be a tendency, perhaps inevitable, to select and weight the desirable evidence, and several statements are made that seem to need much in the way of proof before they can be accepted. As a result few will feel inclined to accept all the author's statements and conclusions.

Reading this book, one cannot help feeling that the interest falls off in the later parts. While dealing with the eastern portions of South Africa, Prof. Bews gives the impression of feeling fully at home, whereas his account of the more western portions, being drawn largely from second-hand information, is much less convincing.

While the book deals exclusively with the flora of South Africa, there is much, especially in the earlier chapters, that is of general interest. The book should certainly serve to stimulate interest in an intricate but very fascinating side of ecological study.

A bibliography of works relating to the South African flora is given and the book has a full index.

R. S. A.

BRITISH ECOLOGICAL SOCIETY

SUMMER EXCURSION 1925

The summer field meeting was held at Aberystwyth where 17 members and some visitors assembled on August 10. The Headquarters were at the Alexandra Hall of Residence where most of the party were accommodated. A very interesting week was spent, in spite of somewhat unfavourable weather, under the guidance of Prof. Stapledon and Prof. Lloyd Williams.

On the first evening a meeting was held at which Prof. Stapledon gave an account of the work of the Welsh Plant Breeding Station and its relation to some of the ecological problems of the district. Much of the mountain area inland from Aberystwyth is covered with grasslands which are heavily grazed by sheep, and it is important to ascertain the effects of constant grazing on different species and varieties of grasses. The methods of investigation and some of the results were described. Other branches of the work of the station were described including the production of new races of grasses, cereals and clovers by hybridisation, and the study of the effects of altering the normal period of daily illumination on different plants. Prof. Lloyd Williams gave an account of some features of interest in the vegetation of the district and of the mode of occurrence of the chief woodland types in the area.

The first day was spent in visits to the Plant Breeding Station, where many things of interest were seen. Mr Tincker demonstrated some of his experiments on the effects of illumination (cf. *Annals of Botany*, 1925) and showed how considerable were the results of growing plants in conditions under which they were exposed to sunlight for a shorter period than that of the normal day. This treatment affected the habit of the plants, their time of flowering and their carbohydrate content. Experimental plots containing clover and cereal hybrids were visited and experiments on the grazing and cutting of grasses were demonstrated.

On the second day the party paid a visit to Plynlimmon with the intention of studying the types of grassland of that district. Most of the observations made, however, related to the climatic conditions of the region as members had full opportunity of realising the exposure of these slopes to wind and the amount of rainfall which may occur on a summer's day.

The wooded valleys between the uplands and the coast were next visited under the guidance of Prof. Lloyd Williams. Most of these were probably covered at one time with *Quercus sessiliflora* woods, though *Quercus robur* woods are found in a few places. In several localities the effects of recent felling were observed. In some places the oaks were growing up from the old stools, while in others the steep hillsides appeared to have become almost bare of vegetation. An interesting case was pointed out where an area seemed to be in process of invasion by *Ulex*. The route taken was up a valley containing several old lead mines and the poisonous effects of the small traces of lead salts in the drainage water were very noticeable. Not only were algae and aquatic plants almost absent from the main river but the colonisation by plants of the recent deposits and gravels seemed to be greatly retarded. The beautiful oak woods at the Devil's Bridge were found to be very interesting. They cover the steep sides of narrow valleys and being very moist they possess a very large and varied cryptogamic flora. Large tufts of *Polypodium vulgare* with many mosses and liverworts growing epiphytically on the trees were conspicuous features, and several of the less common species of British ferns were seen.

The last excursion was to the great Borth bog and to the salt marshes of the Dovey estuary. Parts of this area have been already described (Yapp and Johns in this JOURNAL, 5, 1917 and 10, 1922), but other interesting features were also seen. A brief period was spent on the bog, where the three British *Droseras* were collected. The changes in the vegetation due to peat digging and the subsequent succession were noted. After visiting the salt marshes, the party proceeded to the great shingle bank at the mouth of the estuary where traces of the old hooks or lateral banks were pointed out on the golf links. Near this point an interesting isolated pool was shown to the members and the zonation of its vegetation explained, it contains in one place a vigorous growth of a *Chara*, a plant type which is very rare in the neighbourhood.

During the four days devoted to excursions many varied and interesting types of vegetation were seen and a considerably longer period might have been profitably devoted to their examination. It is hoped however that in the near future further studies on the vegetation of the district will be published by the members of the University of Wales connected with the Botanical and Agricultural departments at Aberystwyth.

H. H. T.

ANNUAL MEETING, MANCHESTER, 1926

The 12th Annual Meeting was held in the Botanical Department of the University, Manchester, on January 9th, 1926. The President, Prof. F. E. Weiss, occupied the Chair.

After the minutes of the previous Annual Meeting had been read and confirmed the President read a letter from Prof. Schroeter in which he expressed his great appreciation of the action of the Society in electing him an Honorary member.

The Treasurer then presented the accounts for 1925 (p. 171), and pointed out that the favourable financial position, by far the most favourable in the history of the Society, was largely due to the great increase in the sales of back numbers and that the year's expenses were not covered by members' subscriptions and sales of the *current volume* of the Journal. The large receipts from the sales of back volumes really represented realisation of capital assets. On the proposition of Prof. Thoday seconded by Dr Woodhead the accounts were formally adopted.

A hearty vote of thanks was accorded to Mr Paulson for auditing the accounts and by a unanimous vote he was elected auditor for the ensuing year. A hearty vote of thanks was also accorded Mr Boyd Watt for his admirable conduct of the finances of the Society.

The Hon. Secretary then submitted his Report, which was adopted.

HON. SECRETARY'S REPORT FOR THE YEAR 1925

During the past twelve months three meetings of the Society have been held. The Annual Meeting took place at University College, London on January the 10th and was preceded by a Soirée in the Botanical Department of which an account has already appeared in our Journal.

The chief Field Meeting was held at Aberystwyth from August 10th–15th under the able guidance of Prof. Lloyd Williams and Prof. Stapledon to both of whom the Society is indebted for the admirable arrangements for the comfort of those who took part. The annual Foray in conjunction with the Mycological Society was held at Burnham Beeches, and for the conduct of this we were again indebted to Mr Ramsbottom.

Two numbers of the Journal have been issued during the year, in February and September respectively, together comprising 336 pages and 14 plates. This it may be pointed out is a larger total than when the Journal was issued in four parts and indeed is nearly equal in size to the issue of last year, for which a special donation was received. It should therefore

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR 1925

[illegible]

BALANCE SHEET AT 31ST DECEMBER, 1925

<i>Liabilities</i>		<i>Assets</i>	
£	s. d.	£	s. d.
Subscriptions prepaid for 1926	Westminster Bank—Credit Balances:	
<i>General Revenue Account</i> —Balances		Current Account ...	24 4 8
Surplus at 31st December, 1924	Deposit Account ...	220 0 0
Surplus from Revenue Account, 1925	147 16 7		
		<i>Journal of Ecology:</i>	
	240 19 5	Credit Note from Publishers
		Note. A further asset is the unsold stock of the <i>Journal</i>	...
		of <i>Ecology</i> held for the Society by the Publishers.	...
			244 4 8
			4 4 9
			<hr/> 248 9 5 <hr/>

I have examined the accounts for the year ending 31st December, 1925, and certify them to be a correct statement and that all vouchers are in accordance with the receipts and payments shown therein.

6th January, 1926.

Hon. Treasurer.

ROBERT PAULSON.

be a matter for gratification to members that whilst the Council deem it necessary to raise the price to non-members in conformity with the actual cost of production, it is still possible to supply the Journal to members without raising the subscription and, so far as the Council can foresee, that necessity is not likely to arise.

We regret to have to record the loss by death of three of our members. Miss Winifred Smith, who endeared herself to all those with whom she came in contact, is a loss that will be keenly felt by many, and particularly by her colleagues at University College, London, of which she was Tutor to women students. Mr Frank Morey, who, like Miss Smith, joined the Society at its inception, was one of that rapidly disappearing class of naturalists whose knowledge and sympathies embrace most branches of Field Natural History. He was the founder and mainstay of the Isle of Wight Natural History Society, to which his loss is an irreparable misfortune, but he has left a permanent memorial of his work in the Island, in his *Natural History of the Isle of Wight*. Mr L. W. Cole, whose untimely death occurred in the early part of the year, was an ecologist of some promise who collaborated in a study of the vegetation of English Heaths, part of the results of which have been published in our Journal.

Five members have tendered their resignations but we welcome in their stead nineteen others who have joined since our last Annual Meeting. The membership is now 166 ordinary members and three Honorary members.

FURTHER RISE IN PRICE OF THE JOURNAL OF ECOLOGY

The President then moved from the Chair the Council's recommendation that the cost of the Journal to non-members should be raised to 30s. Dr Watson spoke against the motion, which he thought would affect foreign subscriptions adversely. Dr Salisbury called attention to the fact that the cost of production of the Journal was in excess of the income derived from the sale of the current volume, and it was therefore only fair that non-members should contribute in money in place of the personal service contributed by members. The motion was then put to the meeting and was carried with one dissentient vote.

ELECTION OF OFFICERS, ETC.

The Meeting then proceeded to the election of Officers as follows:

PRESIDENT: Dr Woodhead.

VICE-PRESIDENT: Dr H. Hamshaw Thomas.

COUNCIL MEMBERS: Prof. Bews, Mr Ramsbottom, Prof. Yapp.

HON. EDITOR: Mr Tansley.

HON. SECRETARY: Dr Salisbury.

The following were elected members:

Mrs Bacon, Miss Gertrude Connolly, Dr G. Jessop, Mr F. S. Laughton and Mr J. Rees.

SCIENTIFIC PROCEEDINGS

Dr W. G. Smith then communicated a paper on the Improvement of Hill Pasture, in the course of which he drew attention to the effect of burning as an amelioration rather than as a permanent improvement and the comparative permanence of the burn limits. The distribution of *Juniperus* on the area in question was attributed to the freedom from fire of the areas where this plant is present. The effects of various manurial treatments were described.

Miss V. E. L. Anderson dealt with some aspects of the Water relations of the Vegetation of the Chalk. The natural water content of the soil of a Chalk Down had been determined at four successive levels at intervals of a fortnight or less throughout a period of eighteen months, which included one year of exceptionally high rainfall and also a period of prolonged drought. The water content was found to have an average value of 36.7 % at the surface and 27.2 % at a depth of 2 ft. 6 ins. The extreme values for the surface were 61.2 % and 8.58 %. The relations of the water content to meteorological and soil conditions were dealt with and the results of a study of the depth and extent of the root systems of the chalk flora were briefly outlined. Whilst a number of species, such as *Polygala vulgaris*, are shallow rooting the root systems of *Poterium sanguisorba* and other of the perennials may attain a depth of over 33 ins.

Mr O. W. Richards read a paper on Animal and Plant Habitats in which he emphasised the difficulty of correlating the communities of animals and plants. The plant community embraced a complex of animal habitats and extensive subdivision of the former was necessary before any clear relation between the two could be established. Owing to the "food cycle" of animals the presence of a species depended not only on the conditions favourable for itself directly but on those favourable to its source of food. Animals were therefore regarded as occupying "niches" rather than habitats.

Mr S. K. Mukerje gave an account of the plant communities found in the Kashmir Himalayas between 5000 and 18,000 ft. Several of the communities described were similar to those of Britain, such as the Phragmitetum, Scirpetum, Typhetum and Fen. The differentiation of these aquatic communities was regarded as depending chiefly upon the depth and translucency of the water and upon the degree of sedimentation. The Xerarch and Hydrarch successions culminate in a mesophytic community dominated by *Cedrus deodara*. Above this latter, which attains to 8000 ft., forests of *Abies webbiana* and *Betula utilis* are followed by Juniper scrub and alpine pasture.

Dr Woodhead described the results of examinations of peat made recently in the Pennines which showed that the peat was already being formed in late Neolithic times. The Roman remains rest on a considerable deposit of peat whilst above these peat of considerable thickness has been formed.

The last paper was a communication of Prof. Oliver in which he described the extensive area at the mouth of the Havre colonised by *Spartina Townsendii*. The chief feature of interest is that the *Spartina* is here followed by *Glyceria maritima*, the first recorded example of a succession initiated by the Rice grass.

The meeting terminated with a hearty vote of thanks to Prof. Weiss and his colleagues for their hospitality and for arranging the exhibition the previous evening.

LIST OF MEMBERS (9 JANUARY, 1926)

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SPHAGNUM BOGS OF CENTRAL RUSSIA: PHYTO- SOCIOLOGY, ECOLOGY AND SUCCESSION

By N. J. KATZ.

(With five Figures in the Text.)

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PREFACE

The data presented in this paper were obtained by my researches in the Governments of Moscow (district of Bogorodsk and Dmitrov), Wladimir (district of Wladimir) and Ivanovo-Voznessensk (districts of Teikof, Sereda, Ivanovo-Voznessensk and Shouja). The total area of the Sphagnum bogs investigated exceeded 400 sq. km. The scanty literary material concerning the former Government of Riazan¹ (1) and that of Tver (2, 3), as well as information directly obtained from A. J. Bronzoff about the former Government of Jaroslav (now Rybinsk) points to a complete analogy between the Sphagnum bogs of these provinces and those I visited myself. It is thus highly probable, that the information given in this paper is also applicable to the greater part of that vast region of Middle Russia which, according to P. Maievsky (4),

¹ This part of the Government of Riazan has now been joined to the Government of Moscow.

extends over the following Governments¹: Moscow, Tver, Jaroslav, Kostroma, Wladimir, Nijni-Novgorod, Riazan, Kaluga, Smolensk, Orel and Penza. Only a few communities of northern plants (*Empetrum nigrum*, *Rubus chamaemorus*, and a few others) belong exclusively to the northern part of this region and are not found in the south. The immense majority belong to the *Sphagnum* bogs of the whole region, except perhaps those of Orel and Smolensk.

My investigations were made in 1917–21. The results have as yet been published in part only (in Russian), (5), (6), (7), (8).

INTRODUCTION

Rübel (9) distinguishes four branches of the study of vegetation:

- (1) Isolation of plant communities and the study of their constitution (Gesellschaftsmorphologie).
- (2) Distribution of communities in space (Chorologische Soziologie).
- (3) Ecology of communities (Ecologische Soziologie).
- (4) Succession of communities (Genetische Soziologie).

To me it seems that no study of the ecology of communities is possible without a knowledge of the ecology of the species which form them, so that questions touching the ecology of species will here take a prominent place.

If we exclude researches which are antiquated in method and give only disjointed and by no means typical lists of species, and also those which touch mainly on palaeontological and stratigraphical questions, there remain very few monographs (1, 2) which contain accounts of the origin and stratigraphical structure of the bogs, of the botanical and chemical composition of the peat, and give descriptions of the vegetation. There does not yet exist in Russian botanical literature any list of the principal plant communities of the *Sphagnum* bogs of Central Russia, much less anything approaching a complete characterisation of these communities.

I shall therefore endeavour, by synthesising the description of various observed plots, to define, for the first time, these communities and to enumerate the species which characterise them. It is also necessary to describe the situations of the communities on the bog surface and the relative areas they occupy (Fig. 1). It was impossible in the time at my disposal to employ exact methods such as "Linientaxering," as used by the Swedish botanist Thore Fries for instance (see H. Osvald, 11), and I have therefore made an approximate estimation of the relative surfaces occupied by the different communities, as shown in the diagram.

The ecology of the bog species, as I understand it, has scarcely been studied at all, either in the region dealt with here, or in Russia generally. The observations of D. A. Gerassimoff (1, 2) concern only a few bogs, i.e. they were made on a comparatively small area. Exact knowledge of the ecological

¹ It is unnecessary to deal with the southern and south-eastern Governments of this part of Russia since hardly any *Sphagnum* bogs occur in them.

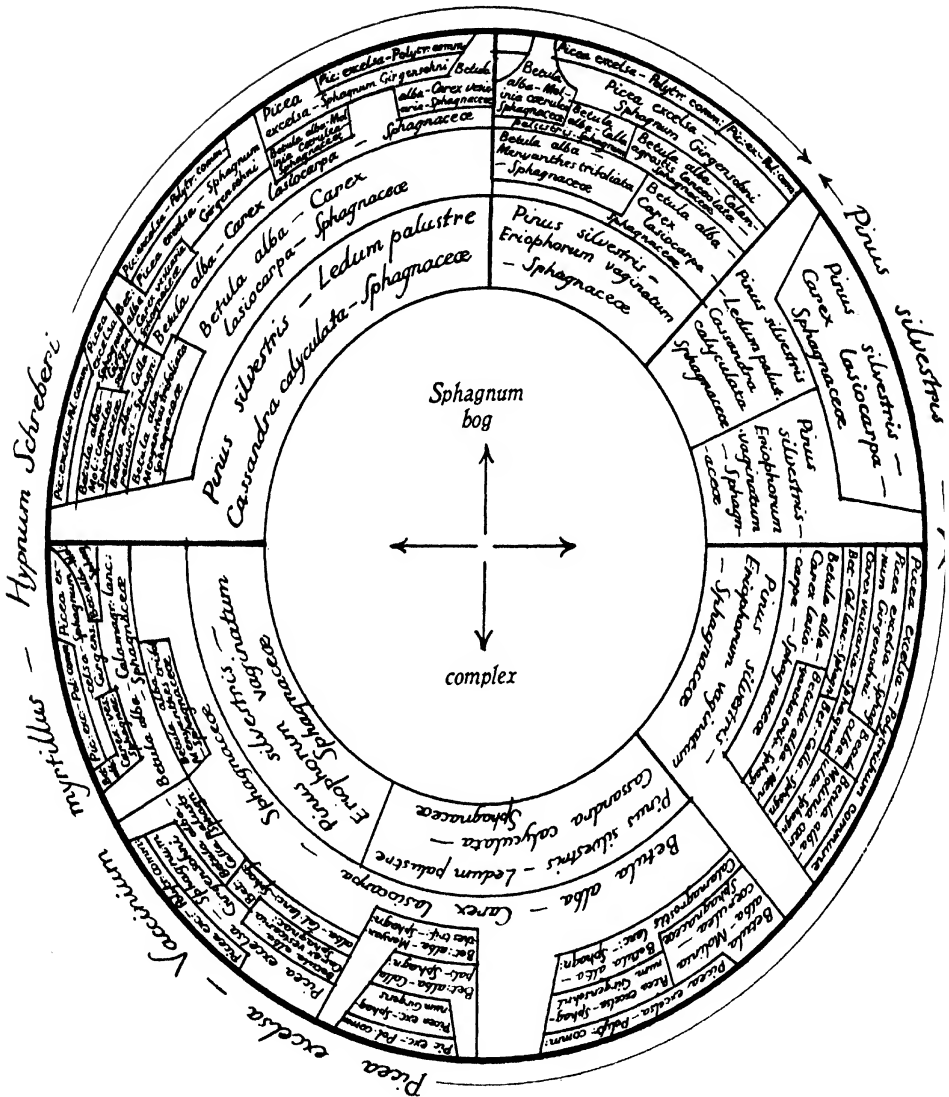


FIG. 1. Diagram illustrating the arrangement of associations of a *Sphagnum* bog developing in the midst of spruce and pine forest. The central space represents the *Sphagnum* bog complex (see text), the arrows indicating the centrifugal march of the associations, which gradually encroach on the forest. The peripheral sectors represent the different associations of the succession from untouched forest to the *Sphagnum* complex. Their areas are roughly proportional to the areas of the different seral associations. One octant represents the succession from pine forest, the remaining seven from spruce forest. It can be seen that the former succession is shorter than the latter, which varies in length, sometimes passing through only two, but often through as many as six stages.

adaptability of species can only be obtained by an examination of extensive material over a wide area.

Again, while the altitudinal zonation, as shown by the microrelief, of the plant communities of meadowland has long been studied in Russia, and is now worked out very minutely (12), the same phenomenon and its relation to the ecology of the bog plant communities of Central Russia have scarcely attracted the attention of investigators, though they represent an important and interesting chapter of phytosociology. My application of the method of "ecological analysis" is also the first in Russian literature, and I am unaware if anything of the kind has been done in other countries.

Likewise the succession of vegetation on the bogs of Central Russia has been but little studied, though Soukacheff (13), Abolin (14), and others have investigated the bogs of north-western Russia from this point of view. The subject has very little in common with botanical researches upon the composition (nature) of peat, which usually give but a schematic picture of the way in which certain types of bog succeed others.

Finally little is known of the varied effects of culture on bog vegetation.

In this paper an attempt has been made to make good these deficiencies so far as was possible during a superficial survey of great areas of bogland, which left no time for the application of exact methods of evaluation of habitat factors. The vegetation is described in terms of the small communities called *associations* by the Upsala school of phytosociologists (Du Rietz, 15), as has already been done by H. Osvald (11) for the *Sphagnum* bog vegetation in Sweden, and the term has been used in this sense throughout the paper¹. My descriptions refer to separate plots of the different associations, but not to quadrats of definite size, as used for instance by the Upsala school (15). The species are arranged according to the strata (Schichten) of the community, beginning with the uppermost. The life forms adopted are as follows:

- md* Deciduimagnolignosa (deciduous trees more than 2 metres high).
- ma* Aciculimagnolignosa (needle-leaved trees).
- p* Parvolignosa (woody plants from .8 to 2 m. high).
- n* Nanolignosa (undershrubs below .8 m.).
- h* Herbaceous plants of non-gramineous type.
- g* Grasses and other plants, such as sedges, of gramineous type.
- b* Leafy mosses and liverworts.
- s* Sphagna.
- l* Lichens.

Degrees of abundance are designated according to Drude's scale. Associations are named according to the dominants of the different strata of the association, and designated by the initial letters of the names of these dominants. In characterising the three fundamental types (Marsh or Fen,

¹ It should be noted that this use of the term 'association' is quite different from that current in most countries, where it is applied to a much larger unit. [Ed.—JOURNAL OF ECOLOGY.]

Niedermoor, Transition bog, *Uebergangsmoor*, and Sphagnum bog, *Hochmoor*) the vegetation itself has been considered first of all, rather than the factors of the habitat (chemical composition of water), or the general aspect (character of bog surface).

The three principal types may be characterised as follows:

1. MARSH or FEN (*Niedermoor*). Dominant and characteristic species: *Alnus glutinosa*, *Betula alba*¹, *Carex caespitosa*, *C. paradoxa*, *C. diandra*, *Aulacomnium palustre*, *Drepanocladus vernicosus*, *Camptothecium nitens*, *Acrocladium cuspidatum*. Sphagna absent or rare. This type chiefly occurs in the river valleys and is fed by ground water rich in mineral salts.

2. TRANSITION BOG (*Uebergangsmoor*). Dominant and characteristic species: *Betula alba* (more rarely *Pinus silvestris*), *Carex lasiocarpa*, *Calamagrostis lanceolata*. Sphagna (chiefly *S. recurvum* (P.B.) Warnst. and *S. subbicolor* Hampe) form a more or less continuous carpet. The type occurs on the edges of Sphagnum bogs or develops in place of (1) along the upper courses of rivers. Water less rich in salts than in (1), partly ground, partly aerial water.

3. SPHAGNUM BOG *sensu stricto* (*Hochmoor*). Dominant and characteristic species: *Pinus silvestris*, *Cassandra calyculata*, *Ledum palustre*, *Andromeda polifolia*, *Eriophorum vaginatum*, *Rhynchospora alba*, *Scheuchzeria palustris*. The dominant Sphagna are *S. medium* Limpr., *S. recurvum*, *S. ballicum* Russ. The type is situated on watersheds and the bog water is poor in salts, being fed by atmospheric water.

1. ECOLOGY OF SPECIES AND OF ASSOCIATIONS

If the quantities of any habitat factor (e.g. distance below the surface of the ground water) are represented as abscissae, and the quantities of a species (e.g. weight developed on a unit area) as ordinates, a curve representing the relation of the species to the given factor (curve of adaptability) may be drawn, the summit of the curve marking the optimum condition of the given factor for the species. If we limit the application to dominant species, it is evident that the range of conditions in which a given species is dominant (amplitude of dominance) is much narrower than the range for isolated individuals (amplitude of occurrence). Here we are chiefly concerned with amplitude of dominance.

The curve of adaptability of a species to a given factor may be modified (a) by the part of the species area under consideration, (b) by the particular complex of environmental factors, (c) by competition.

The researches carried out by myself and S. V. Katz in 1924 on the Tatitshevskoe marsh (Dmitrov district, Gov. of Moscow) show that *Menyanthes trifoliata* is dominant with a ground water depth of 10 to 70 cm., *Carex rostrata*

¹ The name *Betula alba* is used throughout in the aggregate sense. The common form, everywhere dominant in the bog birch forests, is *B. pubescens*; *B. verrucosa* is occasional only.

15–35 cm., *C. limosa* 10–20 cm., *Aulacomnium palustre* 35–60 cm., *Camptothecium nitens* 18–32 cm., *Drepanocladus vernicosus* 10–20 cm. This makes it clear that *Menyanthes* can form communities with all three species of moss mentioned, *Carex rostrata* only with the two latter, and *C. limosa* only with the last, and this is confirmed by study of the communities in nature. Fig. 2 illustrates this. On the horizontal base line are marked the depths of the ground water below the surface, the other horizontal lines (whose varying heights represent the strata of the species) showing the amplitudes in respect of this factor of the six species mentioned. The vertical lines mark the limits of the amplitudes of adaptation of the “associations.”

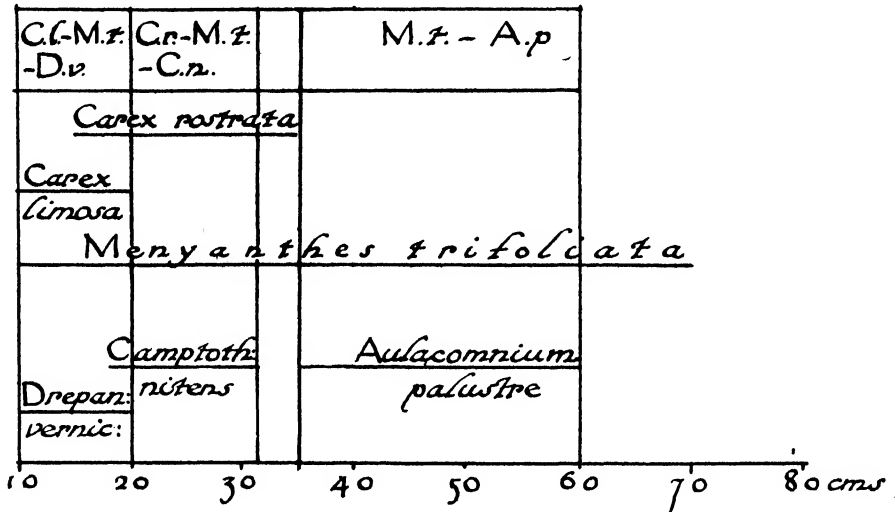


FIG. 2. Diagram showing amplitudes of dominance of certain species and associations with respect to depths of ground water. The top line shows the associations.

Thus the quantitative study of the ecology of species explains, in a general way, why a given species combines in an association with a second species and not with a third, and shows that the ecology of an association, the amplitude of its adaptability, depends in the first place on the ecology of the species constituting it (at least so far as bog associations are concerned). Finally, the amplitude of adaptability of species explains in great measure their capacity for participating in a greater or smaller number of associations.

An ecologist possessing enough quantitative data could foretell, with sufficient probability, the possible combinations of species in associations, and the main lines of their composition and ecology¹. The establishment of quantitative ecological characterisations is work of the future, but even com-

¹ There is good ground for believing that the mutual action of plants upon one another has but a secondary importance in the constitution of bog plant associations. The habitat factors, which group into associations species with a definite amplitude of adaptability, are decisive. I possess a certain number of data supporting this belief.

parative qualitative characterisations are of value to the phytosociologist. An example will illustrate this. On the Tatischevo marsh *Carex limosa* is dominant in water of 20 (German) degrees of hardness, and rich in iron. On the Sphagnum bogs *C. limosa* is dominant in hollows where the water contains a minimum of CaO and iron. Thus the amplitude of this species in respect of these factors is very wide. But in respect of moisture it is very narrow, for *C. limosa* is dominant only when the depth of the ground water is between 10 and 20 cm. It is thus evident that this species can form an association equally well with *Sphagnum balticum* Russ. in a Sphagnum bog, and with *Drepanocladus vernicosus* in a marsh. Both soils have high water content but the soluble salt content is widely different. A ground water depth of 20 cm. marks the extreme limit for the growth of trees, so that it is easy to understand why *Carex limosa* is not met with in forest bogs.

The study of the ecology of species on these lines also gives us a means of establishing ecological series of associations through the use of *plant indicators*. This method, which I call *ecological analysis* of associations, was first used by myself in conjunction with S. V. Katz on the Tatischevo marsh in 1924 in the analysis of experimental quadrats of definite size. Here it is used for the analysis of separate plots differing in size. I am unaware whether the method has been employed elsewhere in Russia or abroad. *Indicators* are for the most part species with a narrow amplitude of adaptability to a given environmental factor. For "moisture series" it is convenient to employ as indicators, on the one hand, species which inhabit mineral soil, and, on the other, species for which excess of moisture gives optimum conditions. The number of indicators of each group on each plot of the association is counted, and the mean number of indicators for each plot is calculated. If the number of plots be sufficient their difference of size has no effect on the final result. The closer the ecological relationship between the associations studied, the more difficult it becomes to choose the indicators, the more sensitive they must be, and the fewer they will be in number.

2. SPHAGNUM BOG (HOCHMOOR)

A. ASSOCIATIONS.

In Central Russia Sphagnum bogs occupy an enormous area comprising thousands of square kilometres and exceeding that of the Marshes and Transition bogs taken together. In consequence of the small number of species dominant in the Sphagnum bogs, the number of associations is also very limited. Association-complexes¹ have a wide extension, and their vegetation consists of small plots of different composition, a few metres square, and alternating with one another, which represent associations or association-fragments¹. The distribution of these is connected with the microrelief of the bog, which is very disjointed. There are high tussocks which may be more

¹ Upsala terminology. [Ed.—JOURNAL OF ECOLOGY.]

than 5 m. in diameter, or the elevations may take the form of low ridges running parallel in a certain direction and anastomosing. The width of these ridges does not exceed 2 m., but their length is often great. The higher tussocks and ridges may be 70 cm. above the bog surface, and between are wet hollows. Sometimes the tussocks or ridges have the appearance of islands in a flat swampy bog, sometimes they are so close together that the wet depressions between are like narrow valleys.

The summits of the highest tussocks and ridges are covered by the association *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sphagnaceae, the sides by *Pinus silvestris-Eriophorum vaginatum*-Sphagnaceae. The hollows are often filled by a mixed association, where *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris* are dominant. Sometimes the vegetation of the hollow is zoned, the outer zone consisting of *C.l.*-Sph., the inner of *Sch.p.*-Sph. Occasionally another association, *Rhynchospora alba*-Sph., occurs between *P.s.-E.v.*-Sph. and *C.l.*-Sph., occupying the peripheral parts of the hollows.

The association-complexes described establish themselves in the centres of the Sphagnum bogs, occupying not less than half the whole area of the Sphagnum and Transition bogs. No detailed description of them exists in Russian literature except in my own papers (5, 6). On the periphery of these association-complexes a uniform vegetation occupies a considerable space. Here we have the associations *P.s.-L.p.-C.c.*-Sph. and *P.s.-E.v.*-Sph., more rarely *C.l.*-Sph.

The following are lists of the species of the associations above mentioned.

The abundance indications follow Drude: *soc.* social, *cop.* copious, *spar.* sparse, *sol.* solitary. The numbers represent percentages of all the plots in which the species occur with the designated abundance.

1. Association *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sphagnaceae. (Compound list from sixteen separate plots.)

- | | |
|---|--|
| <i>ma.</i> <i>Pinus silvestris</i> cop. 25; spar. 75 | <i>g.</i> <i>Melampyrum pratense</i> sol. 6.3 |
| <i>Picea excelsa</i> sol. 7 | <i>Eriophorum vaginatum</i> spar. 44; sol. 44 |
| <i>md.</i> <i>Betula alba</i> sol. 25 | <i>Rhynchospora alba</i> sol. 12.5 |
| <i>n.</i> <i>Ledum palustre</i> cop. 31; spar. 62.5; sol. 6.5 | <i>Scheuchzeria palustris</i> sol. 6 |
| <i>Cassandra calyculata</i> cop. 31; spar. 57; sol. 12 | <i>b.</i> <i>Hypnum schreberi</i> sol. 25 |
| <i>Andromeda polifolia</i> sol. 69 | <i>Polytrichum strictum</i> sol. 25 |
| <i>Vaccinium uliginosum</i> cop. 6.2; sol. 31.3 | <i>Dicranum bonjeani</i> sol. 12.5 |
| <i>V. vitis-idaea</i> sol. 37.5 | <i>a.</i> <i>Aulacomnium palustre</i> sol. 6 |
| <i>V. myrtillus</i> sol. 12.5 | <i>Sphagnum medium</i> soc. 19; cop. 75; spar. 6 |
| <i>Rubus chamaemorus</i> spar. 6.2; sol. 6.3 | <i>S. recurvum</i> (P.B.) Warnst. soc. 19; cop. 69; spar. 12 |
| <i>Vaccinium oxycoccus</i> sol. 81.2 | <i>S. fuscum</i> sol. 12 |
| <i>V. microcarpum</i> sol. 12.5 | <i>S. acutifolium</i> sol. 6 |
| <i>h.</i> <i>Drosera rotundifolia</i> sol. 37.5 | <i>l.</i> <i>Cladonia rangiferina</i> sol. 6 |

2. Association *Pinus silvestris*-*Eriophorum vaginatum*-Sphagnaceae.

(Compound list from eighteen separate plots.)

- | | |
|---|---|
| <i>ma.</i> <i>Pinus silvestris</i> cop. 17; spar. 28; sol. 33 | <i>Scheuchzeria palustris</i> spar. 5·5; sol. 11 |
| <i>md.</i> <i>Betula alba</i> sol. 17 | <i>Carex limosa</i> sol. 11 |
| <i>n.</i> <i>Cassandra calyculata</i> spar. 11; sol. 83·5 | <i>C. pauciflora</i> sol. 11 |
| <i>Andromeda polifolia</i> sol. 78 | <i>C. rostrata</i> sol. 5·5 |
| <i>Ledum palustre</i> sol. 44·5 | <i>C. lasiocarpa</i> sol. 5·5 |
| <i>Vaccinium vitis-idaea</i> sol. 17 | <i>Rhynchospora alba</i> sol. 5·5 |
| <i>V. uliginosum</i> sol. 5·5 | <i>b.</i> <i>Polytrichum strictum</i> sol. 28 |
| <i>V. myrtilhus</i> sol. 5·5 | <i>Hypnum schreberi</i> sol. 22 |
| <i>V. oxycoccus</i> sol. 89 | <i>a.</i> <i>Sphagnum recurvum</i> (P.B.) Warnst. |
| <i>h.</i> <i>Drosera rotundifolia</i> sol. 50 | soc. 28; cop. 50; spar. 16·5; sol. 5·5 |
| <i>D. obovata</i> sol. 5·5 | <i>S. medium</i> Limpr. soc. 22; cop. 22·5; |
| <i>Orchis maculata</i> sol. 5·5 | spar. 22·5; sol. 27·5 |
| <i>Melampyrum pratense</i> sol. 5·5 | <i>S. fuscum</i> cop. 5; sol. 11 |
| <i>g.</i> <i>Eriophorum vaginatum</i> soc. 11; cop. | <i>S. acutifolium</i> sol. 17 |
| 64; spar. 25 | |

These two associations (1 and 2) occupy two-thirds of the total surface of the Sphagnum bogs: each forms little plots of a few square metres in the complexes: in bogs with uniform vegetation each occupies large areas of hundreds or thousands of square metres.

3. Association *Carex limosa*-Sphagnaceae. (Compound list from eleven separate plots.)

- | | |
|---|---|
| <i>ma.</i> <i>Pinus silvestris</i> sol. 9 | <i>g.</i> <i>Carex limosa</i> cop. 45·5; spar. 54·5 |
| <i>Picea excelsa</i> sol. 9 | <i>Scheuchzeria palustris</i> spar. 41; sol. 50 |
| <i>md.</i> <i>Betula alba</i> sol. 9 | <i>Eriophorum vaginatum</i> sol. 54·5 |
| <i>n.</i> <i>Cassandra calyculata</i> sol. 91 | <i>Rhynchospora alba</i> sol. 45·5 |
| <i>Andromeda polifolia</i> sol. 91 | <i>Carex rostrata</i> sol. 27 |
| <i>Vaccinium oxycoccus</i> sol. 54·5 | <i>C. lasiocarpa</i> sol. 9 |
| <i>Salix myrtilloides</i> sol. 9 | <i>b.</i> <i>Hypnum fluitans</i> sol. 9 |
| <i>h.</i> <i>Drosera anglica</i> sol. 9 | <i>Polytrichum strictum</i> sol. 9 |
| <i>Naumburgia thyrsiflora</i> sol. 9 | <i>s.</i> <i>Sphagnum balticum</i> soc. 100 |
| <i>Orchis maculata</i> sol. 9 | <i>S. recurvum</i> (P.B.) Warnst. sol. 18 |
| <i>Menyanthes trifoliata</i> sol. 9 | <i>S. medium</i> sol. 18 |

This association (3) occupies much less space than the two preceding ones.

4. Association *Scheuchzeria palustris*-Sphagnaceae. (Compound list from seven separate plots.)

- | | |
|---|--|
| <i>ma.</i> <i>Pinus silvestris</i> sol. 28·5 | <i>Carex limosa</i> cop. 7; spar. 14·5; sol. |
| <i>md.</i> <i>Betula alba</i> sol. 14 | 64·5 |
| <i>n.</i> <i>Cassandra calyculata</i> sol. 71 | <i>Rhynchospora alba</i> cop. 7; spar. 21; |
| <i>Andromeda polifolia</i> sol. 57 | sol. 29 |
| <i>Vaccinium oxycoccus</i> sol. 57 | <i>Carex rostrata</i> sol. 28·5 |
| <i>h.</i> <i>Drosera rotundifolia</i> sol. 14 | <i>C. lasiocarpa</i> sol. 14·5 |
| <i>D. anglica</i> sol. 14 | <i>s.</i> <i>Sphagnum balticum</i> soc. 100 |
| <i>D. obovata</i> sol. 14 | <i>S. recurvum</i> (P.B.) Warnst. sol. 18 |
| <i>g.</i> <i>Scheuchzeria palustris</i> cop. 50; spar. 50 | <i>S. medium</i> sol. 14 |
| <i>Eriophorum vaginatum</i> sol. 57 | <i>S. dusenii</i> spar. 14 |

This association (4) far from occurring everywhere only exists in little plots. It also often forms quagmires (Schwinggrasen) on peaty lakes surrounded by Sphagnum bog. On the whole the area it occupies is small.

The association (5) *Rhynchospora alba*-Sphagnaceae occurs in little plots in the hollows of the complexes. It also forms but a small share of the bog surface.

B. ECOLOGY OF THE SPECIES (cf. Fig. 4).

Pinus silvestris is the least exacting tree as regards the content of the soil in mineral salts. It is dominant alike on dry sands and on the moist peat of the Sphagnum bogs, substrata alike poor in mineral salts. *Betula alba* grows chiefly in the Transition bogs which are richer in mineral elements. Ground water at a level of 15 to 20 cm. below the surface is the limit for the presence of *Pinus*, and it only forms an association when the ground water level is lower (30 to 40 cm.). This explains the dominance of *Pinus* only in the drier associations, *P.s.-L.p.-U.c.-S.* and *P.s.-E.v.-S.* It is rare in the wetter associations such as *C.l.-S.*, etc. *Ledum palustre* resembles the pine in its relation to moisture, while *Cassandra calyculata* and *Andromeda polifolia* are more hydrophilous.

The height, growth and closeness of stand (see lists in the last section) of the pine diminish with increase of moisture. Thus in *P.s.-L.p.-C.c.-S.* the average height is 5.9 m. (18 plots), in *P.s.-E.v.-S.* it is 4.2 m. (16 plots). In the associations of the hollows the pine does not attain the size of a tree.

Ledum palustre occurs exclusively on the peat poor in salts of the Sphagnum bogs. Like the pine its optimum moisture is found in the driest association, where it is dominant in the undershrub layer, together with *Cassandra calyculata*. In conditions of greater moisture (*P.s.-E.v.-S.*) it occurs only as isolated individuals, and in the wet hollows it disappears entirely. This species is a constant companion of the pine and grows well under its shade.

Cassandra calyculata. Similar to the last in relation to salts. Optimum moisture also like the last, but constantly met with, though not dominant, in the moist associations of the hollows. Like the last it can bear moderate shading.

Andromeda polifolia, like the two last-named species, is characteristic of Sphagnum bog, though rarely dominant. Its optimum moisture tends to be greater than that of *Cassandra*.

The moisture relations of the three last-named species are graphically represented in Fig. 3. Owing to lack of data as to ground water level the four associations are used to indicate the degree of moisture. They show increase of moisture on the horizontal axis, from left to right, and the percentage of frequency for the three species in the different associations is given on the vertical axis.

Eriophorum vaginatum is also a typical species of the Sphagnum bog, though it may be dominant on peat richer in mineral salts where the three species just described are never dominant. It occurs on Transition bogs which have long been drained, and in clearings of birch forest grown on dry bogs, side by side with plants typical of a mineral soil. It also flourishes on burned

peat. On undrained bog its optimum moisture is greater than that of *Cassandra*, but its moisture curve extends further in both directions than those of the three undershrubs, so that it is dominant both in the water-saturated quagmires of turbaries and also on well-drained peat. This considerable amplitude of adaptability as regards both salts and water explains its participation in so many associations. The abundance of winged seeds it produces accounts for its rôle of pioneer on peat destitute of vegetation, whether inundated turbaries or burned peat areas.

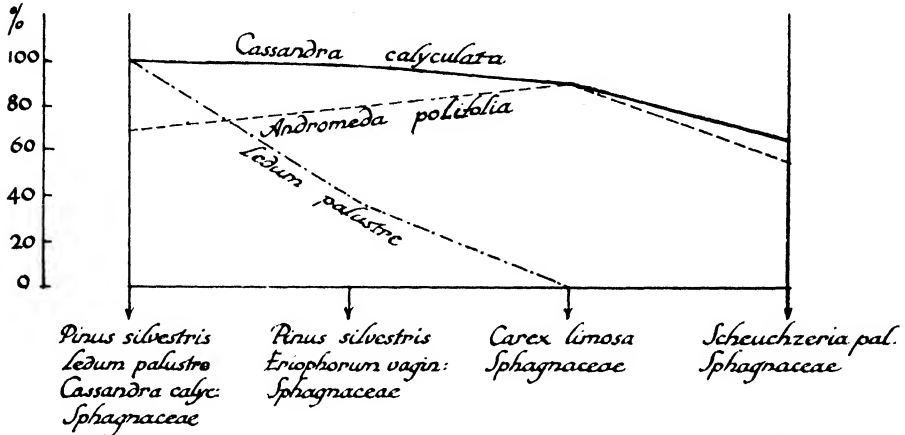


FIG. 3. Graph showing the percentage frequencies of *Cassandra calyculata*, *Andromeda polifolia* and *Ledum palustre* in four associations of the Sphagnum bog.

Scheuchzeria palustris is another typical plant of Sphagnum bog and is confined to the wettest association (*Sch.p.-Sph.*), where the ground water is only a few cm. below the surface.

Rhynchospora alba is again a typical Sphagnum bog species with optimum moisture in *Rh. a.-Sph.*, the moisture curve descending abruptly in the direction of the drier associations.

Carex limosa is the third species of the wet bog hollows. Its optimum moisture lies between those of the two previous species and as with them the moisture curve descends abruptly.

Sphagnum medium Limpr. is dominant only in Sphagnum bogs; in Transition bogs it occurs only as isolated individuals. It is the least hydrophilous of the Sphagna dominant in Sphagnum bog, inhabiting the summits of the tussocks. Its optimum moisture lies in the association *P.s.-L.p.-C.c.-S.*, where it can accommodate itself to moderate shade.

Sphagnum recurvum (P.B.) Warnst. is dominant equally in Sphagnum and Transition bogs. In the Sphagnum bogs var. *parvulum* Warnst., together with *S. ambiphyllum* Russ. var. *parvifolium* Sendt, are chiefly found. I believe they are only xerophytic small-leaved ecological forms of *S. recurvum*, which grow in compact masses on the tops of the tussocks with *S. medium*

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in the *P.s.-C.c.-L.p.-Sph.* association and predominate in the wetter association *P.s.-E.v.-Sph.* on the sides of the tussocks. This is a species of great adaptability as regards quantity of mineral salts and therefore enters many associations. It can bear more shade than *S. medium*.

Sphagnum balticum Russ. is more hydrophilous than the foregoing and is dominant only in the three wet associations of the hollows, its moisture curve resembling that of the three phanerogamic dominants of these associations.

MARSH 6-10%	TRANSITION BOG 5-6%	SPHAGNUM BOG 3.5-5%
P I N U S	S I L V E S T R I S	
B E T U L A	A L B A	SCHUCHZERIA PALUST.
ALNUS GLUTINOSA	CAREX LASIOCARPA	RHYNCHOSP. ALBA
C A R E X	L I M O S A	
C A R E X	R O S T R A T A	ERIOPHOR. VAGINAT.
MENYANTHES TRIFOLIATA		LEDUM PALUSTRE
CALLA PALUSTRIS		CASSANDRA CALYC.
CAREX VESICARIA		
CAREX DIANDRA	MOLINIA CERULEA	
CAREX GRACILIS	CALA MAGROSTIS LANCEOLATA	
CAREX PARADOXA		
CAREX CAESPITOSA		
AULACOMN. PALUSTRE		
CAMPOTHEC. NITENS	SPHAON. SUBBICOLOR	SPHAGNUM MEDIUM
ACROCLADIUM CUSPID.		SPHAGNUM BALTICUM
DREPANOC. VERNICOS.	SPHAGNUM RECURVUM WARB.	

FIG. 4. Amplitudes of adaptability to concentration of mineral salts of species characteristic of Marsh, Transition bog and Sphagnum bog. The percentage figures under these three heads represent, very roughly, the *average percentages of ash* according to Gerassimoff (2), in the peat of the three types. Accurate data on the concentration of salts in the waters are lacking.

Sphagnum Dusenii C. Jensen and *S. cuspidatum* Ehrh. are the most hydrophilous of the Sphagnum bog Sphagna. Sometimes they occur in the wettest hollows of the *Sch.p.-Sph.* association with water above the surface.

Hypnum fluitans (Dill) L. This is the species of *Drepanocladus* most adapted to water very poor in mineral salts, and is the sole representative of the genus met with in great quantity in the Sphagnum bogs of Central Russia. Like most of the species of *Drepanocladus* it has floating forms which inhabit the water of inundated turbaries (see below). The terrestrial forms are very common in drying hollows of the Sphagnum bogs.

C. ECOLOGY OF THE ASSOCIATIONS.

Until recently the importance of moisture as a factor in the distribution of the associations of the Sphagnum bog has been insufficiently recognised, though lately, it is true, classifications of bogs according to moisture have

appeared (16). The very great difference between the conditions of life on the summits of the tussocks and in the hollows close by (an altitudinal difference of about 70 cm.) corresponds with vegetation of quite different species and must be regarded as mainly due to the difference of moisture (5, 6). The altitudinal zonation from the summits of the tussocks to the bottom of the hollows is represented by the series:

<i>P.s.-L.p.-C.c.-Sph.</i>	<i>P.s.-E.v.-Sph.</i>	<i>Rh.a.-Sph.</i>	<i>C.l.-Sph.</i>	<i>Sch.p.-Sph.</i>
summits of tussocks	slopes	sides of hollows		centres of hollows

This zonation based on moisture may be compared with the series obtained by the use of indicators according to the method of "ecological analysis" described on p. 183. Two groups of indicators are chosen: (1) species whose optimum conditions correspond with the lowest ground water level, and (2) species whose optimum conditions correspond with the greatest excess of moisture. To (1) belong *Pinus silvestris*, *Betula alba*, *Picea excelsa*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Ledum palustre*, *Vaccinium uliginosum*, and certain herbaceous species; to (2) *Scheuchzeria palustris*, *Rhynchospora alba*, *Carex limosa*. The average numbers of indicators of the two groups growing in a plot of the four principal associations work out as follows:

	Indicators	
	(1)	(2)
<i>P.s.-L.p.-C.c.-Sph.</i>	3.25	.19
<i>P.s.-E.v.-Sph.</i>	1.78	.33
<i>C.l.-Sph.</i>	.36	2.36
<i>Sch.p.-Sph.</i>	.45	2.43

The indicators of group (1) thus steadily decrease, and those of group (2) increase, in passing from the drier to the wetter associations, corresponding completely with the altitudinal zonation series.

D. SUCCESSION OF ASSOCIATIONS.

Published data (13, 14) on succession in Sphagnum bogs refer only to north-west Russia. Hitherto those of Central Russia have not been studied in respect of succession.

Formation of associations on the periphery of the bogs. The centre of a bog is occupied by an association complex (see p. 183) surrounded by a belt of homogeneous vegetation in which the associations *P.s.-L.p.-C.c.-Sph.* and *P.s.-E.v.-Sph.* predominate. These succeed *Betula alba-Carex lasiocarpa-Sphagnaceae*, and *Pinus silvestris-Carex lasiocarpa-Sphagnaceae*, which are contiguous to them on the edge of the bog (see Fig. 1). The cause of the succession is the overgrowth of the edge of the bog on to the surrounding soil and the consequent giving way of more exacting plants before the advance of less exacting ones. Thus if on the Transition bog *Betula alba* is dominant it will give way before the less exacting *Pinus silvestris*, while if the latter is dominant

it will remain but will be diminished in size and in denseness of stand. Thus in *P.s.-C.l.-Sph.* the mean height of the pines is 6·8 m.: in the Sphagnum bog association *P.s.-L.p.-C.c.-Sph.*, 5·9 m., and in *P.s.-E.v.-Sph.*, 4·6 m. *Carex lasiocarpa*, the dominant herbaceous plant of the Transition bog, is replaced by *Eriophorum vaginatum* and the undershrubs of the Sphagnum bog, while *Sphagnum recurvum* and *S. subbicolor* partly give way to the less exacting *S. medium*. The microrelief becomes more diversified, probably chiefly because *Sphagnum medium* grows more vigorously than *S. recurvum*, so that the former species forms tussocks round the tree trunks which increase in height above the level of the intervening spaces dominated by the more slowly growing *S. recurvum*. Another cause may co-operate in increasing the differences of level. In years of drought the peat *between* the tussocks shrinks the most because it is fuller of water and less dense, while the denser peat of the tussocks shrinks less because it contains less water and is also consolidated below by the tree roots.

A first indication of the age of an association is its position in relation to the centre of the bog—the nearer to the centre the later the stage of succession. Plant indicators may also be used for the analysis of succession. The indicators chosen should be (1) plants of mineral soils, but occurring also in Sphagnum and Transition bogs (*Pinus silvestris*, *Picea excelsa*, *Betula alba*, *Vaccinium myrtillus*, *V. vitis-idaea*, etc.) and (2) typical Sphagnum bog species (*Ledum palustre*, *Cassandra calyculata*, *Andromeda polifolia*, *Eriophorum vaginatum*, *Drosera rotundifolia*, *D. anglica*, *D. obovata*, *Scheuchzeria palustris*, *Rhynchospora alba*). The application of the method is the same as in the ecological analysis described in Section C. The results were as follows:

Average numbers of indicators per plot		
	Mineral soil indicators	Sphagnum bog indicators
Associations of Transition bog	<i>B.a.-C.l.-Sph.</i>	2·4
	<i>P.s.-C.l.-Sph.</i>	1·59
Associations of Sphagnum bog	<i>P.s.-L.p.-C.c.-Sph.</i>	3·2
	<i>P.s.-E.v.-Sph.</i>	2·8
		1·88
		4·38
		1·28
		4·05

Thus the two associations of the Sphagnum bog differ from the two of the Transition bog by the smaller number of mineral soil indicators and the larger number of Sphagnum bog indicators. Consequently on a bog in course of formation indicators of the first group decrease and those of the second increase. If the two genetically equivalent associations of the two types are compared this difference does not appear. In each type one of the associations surpasses the other in the number of indicators of *both* groups. This is because there is a greater number of species, owing to the greater dryness, in a plot of *P.s.-C.l.-Sph.* and in a plot of *P.s.-L.p.-C.c.-Sph.* respectively than in a corresponding plot of the other association. These data confirm the results as to relationship of the associations obtained by a study of their situation.

The *Carex limosa*-Sph. association is most often developed from the Transition bog association *Carex rostrata*-Sph. *Carex rostrata* is replaced by the less exacting *C. limosa*, and *Sph. recurvum* yields most of its place to *Sph. balticum*. The whole process takes place in the presence of more moisture than the one described above. The indicator numbers are as follows:

	Mineral soil indicators	Sphagnum bog indicators
<i>Carex rostrata</i> -Sph.	2.40	1.60
<i>C. limosa</i> -Sph.	0.36	3.91

Here again we have the first group of indicators diminishing, the second increasing, confirming the conclusion, derived from its more peripheral position, that the first association is an earlier stage of succession.

Formation of Association-Complexes.

The complexes of Sphagnum bog associations are situated in the central, oldest parts of the large peat bogs (see Fig. 1, p. 179). They occupy no less than half the whole area of the Sphagnum and Transition bogs taken together, and their wide extent demonstrates their durability. Their position, together with the thickness of the peat beneath them, show that they form the final phase of development of the Sphagnum bog vegetation.

The complexes develop from different associations of the peripheral zone, such as *P.s.-L.p.-C.c.*-Sph. and *P.s.-E.v.*-Sph. As soon as *Sphagnum medium* appears on a Transition bog tussocks begin to form and, owing to the rapid growth of this species, attain a considerable size. In the hollows between the tussocks atmospheric water, running down the sides, begins to accumulate, first of all killing the trees in these hollows owing to excess of moisture. Next the undershrubs perish, and the more hydrophilous *Sphagnum balticum* replaces *S. recurvum*. Lastly there appear in the hollows the hydrophilous species *Carex limosa*, *Rhynchospora alba*, and *Scheuchzeria palustris*.

The development of a complex from the association *Carex limosa*-Sph. occurs as follows. In this association there are always small tussocks because Sphagnum grows very energetically round tufts of *Eriophorum*, undershrubs, etc. When the more xerophilous *Sphagnum medium* appears on these tussocks they grow more rapidly and are finally colonised by *Pinus silvestris* and undershrubs, thus forming a complex with the association of the hollows.

Changes of Association-Complexes.

The associations of a complex are not stable but undergo changes which may bring back an earlier phase of development. These changes have been described in north-west Russia by Soukacheff (13) and certain other investigators, in Sweden by Osvald (11) in great detail. In Central Russia the process is different to that which obtains in more northern latitudes.

The Sphagnum carpet of the hollows of undrained peat bogs very often begins to die off over areas of thousands of square metres. This is caused by

periods of hot summer drought, which only affect the *Sphagna* of the hollows, such as *S. balticum*, whose stems then lie horizontally on the peat surface, becoming covered with a crust of algae. The species of the tussocks (*S. medium* and *S. recurvum*) do not suffer from drought though they live in a drier place. Their dense growth enables them to absorb and retain a greater quantity of moisture than the loose growth of *S. balticum*, with its long stems and distant whorls of branches. The whorls of close-set branchlets and the minute leaves of *S. recurvum* form a good water-holding structure, while *S. medium* has a well developed system of pore-bearing hyaline cells. Certainly in Central Russia these tussock *Sphagna* do not die off owing to drought, nor are they replaced by liverworts and lichens as in more northern latitudes.

In hollows thus deprived of their *Sphagnum* covering *Hypnum fluitans* (Dill) L., appears as a pioneer, often producing fruit. Sometimes *Rhynchospora alba* appears on the bare peat ("naked *Rhynchospora alba* moor" of Osvald, 11). The drying up of the hollows favours this species at the expense of its more hydrophilous competitors, *Carex limosa* and *Scheuchzeria palustris*.

If the hollows remain dry, all these associations give place to *Eriophorum vaginatum* on naked peat, which may establish itself at once without the intervention of the pioneers. Tussocks of this species arise from seed coming from the neighbouring hillocks into the hollows, and growing rapidly fill up the hollows with new hillocks. These new tussocks or hillocks become colonised by *Sphagnum medium*, and with the old ones flatten out the microrelief into an approximately level surface (*Eriophorum vaginatum*-Sph. association). In time differentiation of the microrelief begins afresh and the gradual development of a new complex ensues. If the drying of the hollows is only temporary, *Eriophorum vaginatum* does not establish itself and *Carex limosa*-Sph. association re-develops.

3. TRANSITION BOG (UEBERGANGSMOOR)

A. ASSOCIATIONS.

1. Association *Betula alba*-*Molinia caerulea*-Sphagnaceae.

<i>md.</i> <i>Betula alba</i> cop.	<i>Equisetum silvaticum</i> sol.
<i>ma.</i> <i>Pinus silvestris</i> sol.	<i>g.</i> <i>Molinia caerulea</i> cop.
<i>Picea excelsa</i> sol.	<i>Calamagrostis lanceolata</i> sol.
<i>p.</i> <i>Rhamnus frangula</i> sol.	<i>Carex vesicaria</i> sol.
<i>n.</i> <i>Vaccinium vitis-idaea</i> sol.	<i>b.</i> <i>Polytrichum commune</i> sol.
<i>V. myrtillus</i> sol.	<i>Hypnum Schreberi</i> sol.
<i>h.</i> <i>Menyanthes trifoliata</i> sol.	<i>s.</i> <i>Sphagnum recurvum</i> Warnst. cop.
<i>Calla palustris</i> sol.	<i>S. Girgensohnii</i> sol.
<i>Trientalis europaea</i> sol.	<i>S. subbicolor</i> sol.

This association is found in little plots, rarely more than 10 m. square, on the very limit of the Transition bog and the forest on mineral soil. On the whole this association covers an insignificant part of the surface belonging to the Transition bog. Frequently it forms also a narrow ring round the peat lakes, surrounded by *Sphagnum* bogs.

2. Association *Betula alba-Carex vesicaria*-Sphagnaceae.

- | | |
|---|---|
| <i>md.</i> <i>Betula alba</i> cop. | <i>Calla palustris</i> sol. |
| <i>ma.</i> <i>Pinus silvestris</i> sol. | <i>Lysimachia vulgaris</i> sol. |
| <i>Picea excelsa</i> sol. | <i>Equisetum silvaticum</i> sol. |
| <i>p.</i> <i>Rhamnus frangula</i> sol. | <i>g.</i> <i>Carex vesicaria</i> cop. |
| <i>h.</i> <i>Menyanthes trifoliata</i> sol. | <i>Calamagrostis lanceolata</i> sol. |
| <i>Comarum palustre</i> sol. | <i>Carex lasiocarpa</i> sol. |
| <i>Peucedanum palustre</i> sol. | <i>s.</i> <i>Sphagnum recurvum</i> Warnst. soc. |
| <i>Naumburgia thyrsoiflora</i> sol. | |

Like the preceding association, this is met with in little plots on the extreme limit of the Transition bog with mineral soil. The surface it occupies is very small.

3. Association *Betula alba-Calla palustris*-Sphagnaceae.

- | | |
|--|--|
| <i>md.</i> <i>Betula alba</i> spar. | <i>h.</i> <i>Calla palustris</i> soc. |
| <i>ma.</i> <i>Pinus silvestris</i> sol. | <i>Menyanthes trifoliata</i> sol. |
| <i>Picea excelsa</i> sol. | <i>s.</i> <i>Sphagnum recurvum</i> Warnst. spar. |
| <i>n.</i> <i>Cassandra calyculata</i> sol. | |

This association occurs in plots of larger size than the preceding ones, not seldom attaining 100 square m. It also establishes itself in the peripheral belt of the Transition bog, not far from the mineral soil. On the whole it likewise takes up small spaces on the Transition bogs.

4. Association *Betula alba-Menyanthes trifoliata*-Sphagnaceae.

- | | |
|---|---|
| <i>md.</i> <i>Betula alba</i> spar. | <i>Equisetum heleocharis</i> sol. |
| <i>ma.</i> <i>Picea excelsa</i> sol. | <i>Galium palustre</i> sol. |
| <i>n.</i> <i>Salix repens</i> sol. | <i>Caltha palustris</i> sol. |
| <i>S. lapponum</i> sol. | <i>Carex lasiocarpa</i> sol. |
| <i>Betula humilis</i> sol. | <i>Calamagrostis lanceolata</i> sol. |
| <i>Vaccinium oxycoccus</i> sol. | <i>Molinia caerulea</i> sol. |
| <i>Cassandra calyculata</i> sol. | <i>Carex stricta</i> sol. |
| <i>Andromeda polifolia</i> sol. | <i>C. vesicaria</i> sol. |
| <i>h.</i> <i>Menyanthes trifoliata</i> cop. | <i>C. rostrata</i> sol. |
| <i>Naumburgia thyrsoiflora</i> sol. | <i>b.</i> <i>Hypnum schreberi</i> sol. |
| <i>Peucedanum palustre</i> sol. | <i>Hylocomium splendens</i> sol. |
| <i>Comarum palustre</i> sol. | <i>s.</i> <i>Sphagnum recurvum</i> cop. |

This association is found in plots of a considerable size, sometimes of several hundreds of square metres, and is of greater importance for the general aspect of the Transition bogs than any of the three preceding ones. But all four together occupy a very insignificant area compared with the two which follow.

5. Association *Betula alba-Calamagrostis lanceolata*-Sphagnaceae.

(Compound list from seven separate plots.)

- | | |
|--|--|
| <i>md.</i> <i>Betula alba</i> soc. 14; cop. 71-5; spar. 14-5 | <i>Rubus idaeus</i> sol. 14 |
| <i>Populus tremula</i> sol. 14 | <i>n.</i> <i>Cassandra calyculata</i> sol. 14 |
| <i>ma.</i> <i>Pinus silvestris</i> sol. 57 | <i>Vaccinium oxycoccus</i> sol. 14 |
| <i>Picea excelsa</i> sol. 57 | <i>V. myrtillus</i> sol. 43 |
| <i>Salix aurita</i> spar. 14; sol. 57 | <i>V. vitis-idaea</i> sol. 28-5 |
| <i>Rhamnus frangula</i> sol. 28-5 | <i>h.</i> <i>Comarum palustre</i> spar. 14-3; cop. 14-3; sol. 57 |
| <i>Viburnum opulus</i> sol. 14 | <i>Naumburgia thyrsoiflora</i> sol. 71-5 |
| <i>Salix cinerea</i> sol. 14 | <i>Menyanthes trifoliata</i> sol. 57 |

- Peucedanum palustre* sol. 43
Galium palustre sol. 43
Ranunculus lingua sol. 28·5
Equisetum silvaticum sol. 28·5
Melampyrum nemorosum sol. 28·5
Trientalis europaea sol. 28·5
Epilobium angustifolium sol. 14
Pirola rotundifolia sol. 14
Potentilla silvestris sol. 14
Epilobium palustre sol. 14
g. Calamagrostis lanceolata cop. 86; spar. 14
Carex lasiocarpa cop. 14; spar. 14; sol. 29
Phragmites communis spar. 43; sol. 14
Carex canescens sol. 43
Agrostis canina spar. 14; sol. 15
Deschampsia caespitosa sol. 29
Carex vulgaris sol. 29
Juncus effusus sol. 14
Molinia caerulea sol. 14
Carex vesicaria sol. 14
C. rostrata sol. 14
b. Polytrichum commune sol. 28·5
Hypnum schreberi sol. 28·5
Dieranum undulatum sol. 14
Aulacomnium palustre sol. 14
Climacium dendroides sol. 14
Hylocomium splendens sol. 14
s. Sphagnum recurvum soc. 43; spar. 28·5; sol. 28·5
S. squarrosum sol. 28·5

This association occurs in plots of greater extension than any of the preceding and on the whole takes up large areas. It exists almost invariably on *Sphagnum* peat bogs with active peripheral growth and surrounded by forest. Here it forms a band of a few metres in width on the limit of the mineral soil.

6. Association *Betula alba-Carex lasiocarpa*-Sphagnaceae.

(Compound list from seventeen plots.)

- md. Betula alba* cop. 6; spar. 30; sol. 35
Populus tremula sol. 12
ma. Pinus silvestris sol. 53
Picea excelsa sol. 18
p. Salix aurita spar. 6; sol. 35
S. repens sol. 35
S. lapponum sol. 35
S. myrtilloides sol. 23·5
S. cinerea sol. 12
Rhamnus frangula sol. 12
Salix pentandra sol. 6
n. Cassandra calyculata sol. 82·5
Vaccinium oxycoccus spar. 6; sol. 70·5
Andromeda polifolia sol. 35
Ledum palustre sol. 12
Vaccinium vitis-idaea sol. 12
V. myrtillus sol. 12
h. Comarum palustre spar. 18; sol. 53
Menyanthes trifoliata spar. 6; sol. 65
Naumburgia thyrsiflora sol. 53
Peucedanum palustre sol. 47
Equisetum heloccharis spar. 52; sol. 35
Epilobium angustifolium sol. 18
E. palustre sol. 12
Galium palustre sol. 30
Orchis maculata sol. 12
Drosera rotundifolia sol. 12
Calla palustris sol. 6
Scutellaria galericulata sol. 6
Viola epipsila sol. 6
Lysimachia vulgaris sol. 6
g. Carex lasiocarpa soc. 36; cop. 53; spar. 11
Calamagrostis lanceolata cop. 6; spar. 12; sol. 41
Carex rostrata sol. 41
C. limosa sol. 41
C. chordorrhiza sol. 23·5
C. canescens sol. 18
Eriophorum vaginatum sol. 18
E. angustifolium sol. 6
Molinia caerulea sol. 6
Deschampsia caespitosa sol. 6
Carex vesicaria sol. 6
Agrostis canina sol. 6
Phragmites communis sol. 6
b. Polytrichum commune sol. 47
Hypnum schreberi sol. 18
Dieranum bonjeani sol. 6
s. Sphagnum recurvum Warnst. soc. 76; cop. 6; spar. 12; sol. 6
S. medium sol. 18
S. subbicolor sol. 12
S. squarrosum sol. 6

This association occupies a greater surface on Transition bogs than all the other associations taken together. It extends uninterruptedly over considerable areas, not seldom thousands of square metres.

7. Association *Pinus silvestris*-*Carex lasiocarpa*-Sphagnaceae.

(Compound list from five plots.)

- | | |
|---|--|
| <i>md.</i> <i>Betula alba</i> cop. 20; sol. 40 | <i>g.</i> <i>Carex lasiocarpa</i> cop. 90; spar. 10 |
| <i>Populus tremula</i> sol. 20 | <i>Calamagrostis lanceolata</i> cop. 20; spar. 20 |
| <i>ma.</i> <i>Pinus silvestris</i> cop. 60; spar. 20; sol. 20 | <i>Eriophorum vaginatum</i> cop. 20; spar. 20; sol. 60 |
| <i>Picea excelsa</i> sol. 20 | <i>Molinia caerulea</i> sol. 20 |
| <i>p.</i> <i>Salix aurita</i> spar. 40 | <i>Polytrichum strictum</i> sol. 60 |
| <i>n.</i> <i>Vaccinium oxycoccus</i> cop. 20; sol. 60 | <i>Hypnum schreberi</i> sol. 40 |
| <i>Cassandra calyculata</i> spar. 20; sol. 60 | <i>s.</i> <i>Sphagnum recurvum</i> soc. 40; cop. 60 |
| <i>Ledum palustre</i> sol. 60 | <i>S. subbicolor</i> soc. 20; cop. 40 |
| <i>Andromeda polifolia</i> sol. 40 | <i>S. medium</i> sol. 20 |
| <i>Vaccinium myrtillus</i> sol. 40 | <i>l.</i> <i>Cladonia rangiferina</i> sol. 20 |
| <i>V. uliginosum</i> sol. 20 | |
| <i>h.</i> <i>Orchis maculata</i> sol. 20 | |

This association covers considerable spaces on Transition bogs, only surpassed in this respect by the preceding one. It is found in plots of hundreds and thousands of square metres.

8. Association *Carex rostrata*-Sphagnaceae.

(Compound list from five plots.)

- | | |
|--|---|
| <i>md.</i> <i>Betula alba</i> sol. 100 | <i>Carex vulgaris</i> sol. 20 |
| <i>ma.</i> <i>Pinus silvestris</i> sol. 80 | <i>C. canescens</i> sol. 20 |
| <i>Picea excelsa</i> sol. 40 | <i>C. limosa</i> sol. 20 |
| <i>p.</i> <i>Salix aurita</i> sol. 20 | <i>Scheuchzeria palustris</i> spar. 20 |
| <i>h.</i> <i>Menyanthes trifoliata</i> spar. 20; sol. 80 | <i>n.</i> <i>Cassandra calyculata</i> sol. 40 |
| <i>Naumburgia thyrsiflora</i> sol. 40 | <i>Andromeda polifolia</i> sol. 40 |
| <i>Comarum palustre</i> sol. 40 | <i>Vaccinium oxycoccus</i> sol. 40 |
| <i>Epilobium palustre</i> sol. 20 | <i>Ledum palustre</i> sol. 20 |
| <i>Equisetum helocharis</i> sol. 20 | <i>Vaccinium vitis-idaea</i> sol. 20 |
| <i>Calla palustris</i> sol. 20 | <i>b.</i> <i>Hypnum schreberi</i> |
| <i>Galium palustre</i> sol. 20 | <i>Polytrichum commune</i> |
| <i>Utricularia vulgaris</i> sol. 20 | <i>Aulacomnium palustre</i> |
| <i>Alisma plantago</i> sol. 20 | <i>Dieranum bonjeani</i> |
| <i>Ranunculus lingua</i> sol. 20 | <i>s.</i> <i>Sphagnum recurvum</i> soc. 40; cop. 40; spar. 20 |
| <i>g.</i> <i>Carex rostrata</i> soc. 20; cop. 60; spar. 20 | <i>S. medium</i> sol. 40 |
| <i>C. lasiocarpa</i> sol. 60 | <i>S. squarrosum</i> sol. 40 |
| <i>Calamagrostis lanceolata</i> sol. 40 | <i>S. obtusum</i> sol. 20 |
| <i>Carex vesicaria</i> sol. 40 | |
| <i>Eriophorum vaginatum</i> sol. 40 | |

This association often covers hundreds of square metres of treeless Transition bog on mineral soil at the edge of meadow associations, and is the most extensive of treeless Transition bog associations.

The *Menyanthes trifoliata*-Sphagnaceae association (not described here) is the only remaining Transition bog association that plays any considerable part in the general aspect of the vegetation covering.

B. ECOLOGY OF THE SPECIES. (Cf. Fig. 4, p. 188.)

The formation of new peat in the Transition bog exceeds its decomposition and therefore the bog continually grows in height. As this happens the roots of the plants are removed further from the ground water table and are increasingly fed with atmospheric water so that the concentration of mineral

salts in the water feeding the plant roots becomes less and less. The different species show different powers of adapting themselves to this change.

Carex vesicaria grows in company with *C. gracilis* on marshes, and occurs also on Transition bogs which are just forming on mineral soil (cf. Fig. 4). It is dominant mainly in places where water stands in spring, but which are comparatively dry in summer. It is more hydrophilous than *C. gracilis*, so that it occupies lower levels in the microrelief. It stands shading fairly well.

Molinia caerulea occurs as isolated plants on marshes, and, like *Carex vesicaria*, than which it is rather more xerophilous, it forms associations on very recent Transition bogs. It also bears shading fairly well.

Calla palustris has a greater range of adaptation to varying concentration of mineral salts than the two preceding species, so that although it occurs on marshes it also forms an association on older Transition bogs. It is more hydrophilous than *Carex vesicaria* and bears shading well.

Menyanthes trifoliata has an even greater range of adaptability to differences in concentration of mineral salts, so that it is dominant in a number of associations from marshes to older Transition bogs. It also has a great range in respect of adaptation to water. It tolerates shading fairly well.

Calamagrostis lanceolata is dominant only on Transition bogs of the same age as those where *Calla palustris* flourishes. Its relation to water is intermediate between those of *Molinia* and *Calla*. It bears shading fairly well.

Carex lasiocarpa is a typical plant of the Transition bog, very well adapted to the varying conditions of existence on the growing surface of the peat, and can tolerate a lower concentration of mineral salts than any of the preceding species, so that it occurs on older bogs. Rarely (as on the Tatischevo marshes) it is dominant where the hardness of the water rises to 20 (German) degrees. It is more hydrophilous than the preceding species and can bear moderate shading.

Carex rostrata ranges from water of 25 degrees of hardness to bogs slightly younger than those in which *C. lasiocarpa* flourishes. It is more hydrophilous than that species and likes slowly flowing water. It does not tolerate shading.

C. ECOLOGY OF THE ASSOCIATIONS.

The associations of the Transition bog are not genetically equivalent, but form a developmental series beginning with boggy forests and ending with the *Sphagnum* bogs. It is moisture which determines the distribution in space of the associations which are more or less genetically equivalent. The following lists of associations are in order of increasing moisture:

Younger associations

Betula alba-*Molinia caerulea*-*Sphagnaceae*
Betula alba-*Carex vesicaria*-*Sphagnaceae*
 { *Betula alba*-*Calla palustris*-*Sphagnaceae* }
 { *Betula alba*-*Menyanthes trifoliata*-
Sphagnaceae }

Older associations

Betula alba-*Calamagrostis lanceolata*-*Sphagnaceae*
Pinus silvestris-*Carex lasiocarpa*-*Sphagnaceae*
Betula alba-*Carex lasiocarpa*-*Sphagnaceae*
Carex rostrata-*Sphagnaceae*

Using as indicators species of mineral soil which require little water we obtain a series corresponding completely with the moisture series above. With increase of moisture the number of mineral soil indicators decreases.

<i>Betula alba-Calamagrostis lanceolata</i> -Sph.	5.0	<i>Betula alba-Carex lasiocarpa</i> -Sph.	2.41
<i>Pinus silvestris-Carex lasiocarpa</i> -Sph.	3.2	<i>Carex rostrata</i> -Sph.	2.40

The small difference between the last two figures is due to the small number of plots of the last association investigated. The number of plots of the younger associations given in the moisture series above was insufficient for the application of this method of analysis.

D. SUCCESSION OF ASSOCIATIONS.

The associations of the Transition bog are in a state of unstable equilibrium. They form a continuous developmental series, beginning with the associations of the mineral forest or meadow soil and ending with the Sphagnum bog complex. Under existing climatic conditions this process of development, when once it begins, tends to continue to its natural climax, each association making its own continued existence impossible, and furnishing the conditions for the formation of a succeeding one.

There is no doubt that this gradual transformation of forest into bog also took place in former times, and that on a large scale. The layer of Sphagnum-sedge peat with abundant pine wood occurring at the bottom of most of the bogs is evidence that they were formed chiefly by the gradual invasion of coniferous forest by the bog plants. The processes of succession involved, the longest and most complicated of which is the transformation of spruce-birch forest into bog, have not yet been described in any detail for Central Russia. The chief criterion of the position of an association in the genetic series is its relation to the centre of the bog. The nearer it is to the centre the later it stands in the genetic series. Measurement of the thickness of the peat affords indirect confirmation of conclusions reached in this way. The extent of surface occupied is a measure of the relative duration of an association—the greater the area the more long-lived is an association on the whole. The means of propagation of the species must also be considered.

The typical forest association is *Picea excelsa*-*Vaccinium myrtillus*-*Hypnum schreberi* with abundance of *V. vitis-idaea*. The transformation usually begins with the appearance of *Polytrichum commune*. Its dense tufts spread rapidly and stifle the other mosses and the flowering plants. A zone of *Picea excelsa*-*Polytrichum commune*, a few metres wide, commonly occurs in spruce forests which are beginning to be transformed into bog. *Polytrichum commune* retains moisture in its dense tufts and makes possible the establishment of the more hydrophilous *Sphagnum girgensohni*. The *Picea excelsa*-*Polytrichum commune* association gives way to the association *Picea excelsa*-*Sphagnum girgensohni*. Neither of these associations is long-lived. The appearance of *Sphagnum recurvum* P.B. and the beginning of peat formation is accompanied by the

rapid dying off of the spruce, which does not regenerate. *Betula alba* becomes predominant, *Sphagnum recurvum* forms the moss-carpet, and the forest species give way to bog species. This marks the establishment of Transition bog proper.

The associations of the Transition bog are disposed in concentric circles round the centre of the bog (Fig. 1). On the very edge of the mineral soil small islets of *Betula alba-Carex vesicaria*-Sph. and *Betula alba-Molinia caerulea*-Sph. are scattered. The shallowness of the peat, which does not exceed a few centimetres, and the smallness of the areas of these associations, point to their short duration.

Further towards the centre of the bog extend the associations *Betula alba-Calla palustris*-Sph. and *Betula alba-Calamagrostis lanceolata*-Sph. There may be from 15 to 40 cm. of peat under the last-named (Masslovo Bog, District of Bogorodsk, Gov. of Moscow), and this shows that the bog has already passed through decades or even centuries of development, while the considerable size of the areas indicates comparative stability. This association in fact extends almost everywhere along the wooded borders of the bogs.

Next comes the association *Betula alba-Menyanthes trifoliata*-Sph. on still thicker peat, and then a wide belt of *Betula alba-Carex lasiocarpa*-Sph. on peat up to 100 cm. and more in depth, extending over hundreds or thousands of square metres, indicating its relative longevity. This association in fact occupies more space than all the earlier ones (which tend to occur as islands in it) put together, so that we may conclude that its longevity is also greater than that of all the others together. In regard to the fate of *B.a.-C.l.*-Sph., see p. 189.

Individual associations may of course be missing from any given successional series.

Analysis by means of indicators confirms the conclusions drawn from the position of the associations.

	Mineral soil indicators	Sphagnum bog indicators
<i>Betula alba-Calamagrostis lanceolata</i> -Sph.	5.29	1.86
<i>Betula alba-Carex lasiocarpa</i> -Sph.	2.41	3.94

Not enough plots of the genetically earlier associations were examined to enable an indicator analysis to be made.

The succession from pine forest to Sphagnum bog passes through a smaller number of stages than the succession from spruce forest (see Fig. 1). This is because the sandy soil on which the pine forest grows is poorer in mineral salts, so that the last stage can be reached more rapidly. Very often the development begins with the development of a sphagnum carpet with *Carex lasiocarpa* in the pine forest itself (*P.s.-C.l.*-Sph.). Then comes *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sph. or *Pinus silvestris-Eriophorum vaginatum*-Sph. (Fig. 1). Sometimes the succession is still shorter, the pine forest passing directly into a bog, oftenest into *P.s.-L.p.-C.c.*-Sph. (The Birch-*Calamagrostis*-Sph. stage does not occur.)

When treeless meadow develops into bog the association *Carex rostrata*-Sph. appears. This cannot be dealt with here.

4. INFLUENCE OF CULTURE ON THE VEGETATION OF SPHAGNUM AND TRANSITION BOGS

DRAINAGE.

If the drainage is very complete the bog vegetation disappears altogether and the peat becomes inhabited by a varied ruderal flora (*Rumex acetosella*, *Epilobium angustifolium*, etc.). With moderate drainage the bog plants survive but different species show varying degrees of resistance. *Vaccinium uliginosum* is more resistant than most, so that in moderately drained *P.s.-L.p.-C.c.-Sph.*

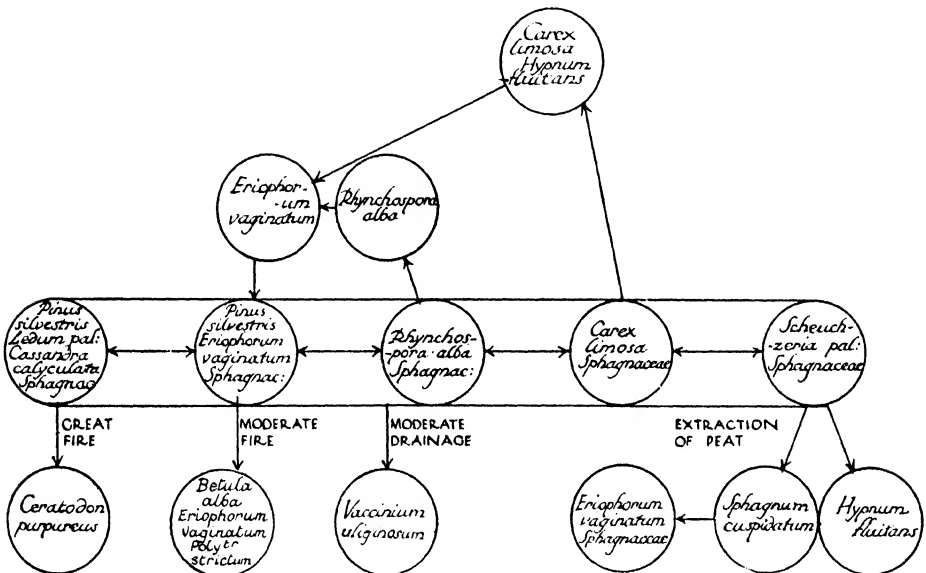


FIG. 5. Transformations of associations of the Sphagnum bog in nature and as a result of artificial interference.

The central horizontal row of five circles represents the changes of the associations of the central bog complex, which may proceed in either direction, from more xerophytic (left) to more hydrophytic (right) or vice versa (see p. 192). The upper circles represent the associations which are formed after the dying off of Sphagnum in the hollows, bringing about the levelling of the uneven microrrelief. The lowest horizontal row represents the changes in vegetation brought about by fires, drainage and peat extraction.

it often predominates (Fig. 5), though playing an altogether subordinate part in the untouched association. I have observed thousands of square metres of luxuriant *V. uliginosum* during the first stages of draining, and even on completely drained bogs where peat is being dug the species occurs in large groups.

Eriophorum vaginatum does not bear drainage so well, though it occurs almost pure along the sides of sufficiently damp turbaries. When the plants are in fruit such places can be picked out from a distance by their dazzling

white colour. The hydrophilous *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris* disappear first on drainage; also the Sphagna, *S. medium* holding out longer than *S. recurvum*.

EXTRACTION OF PEAT (see Fig. 5).

The vegetation of turbaries depends on (1) the type of bog, (2) the thickness of the untouched peat, (3) the depth of water in the turbarry, (4) the age of the turbarry.

The colonisation of Sphagnum bog turbaries which are constantly inundated proceeds as follows. The pioneers are the floating Sphagna (most often *S. cuspidatum*) or the genus or subgenus Drepanocladus (Harpidium), most often *Hypnum* (*Drepanocladus*) *fluitans*. At first the separate moss plants grow horizontally, but gradually, as they multiply and exercise lateral pressure upon one another, they become vertical and the dense mass forms a platform on which *Eriophorum vaginatum* can establish itself. This species colonises easily by its flying seeds always ripening in abundance, and is scattered from the peat heaps left by the extracting engines. On turbaries thirty years old the tufts of *Eriophorum* are usually in lateral contact, but with their bases separated by a quagmire covered by Sphagnum which hides the surface of the water (Fig. 5). *Carex limosa* is absent from this habitat which seems most suitable for it. The explanation is that this species disappears from the bog as soon as drainage begins and its seeds are too heavy to travel any distance.

On the turbaries which are not inundated forest of *Betula alba* develops with a ground vegetation of various marsh-loving species.

The colonising vegetation depends also on the proportion of mineral salts in the water and on its reaction. Poverty in mineral salts and an acid reaction are favourable to the development of Sphagnum bog plants. The inundated turbaries of Transition bogs, especially those with a mineral bottom, are colonised by aquatic plants, most often *Hydrocharis morsus-ranae*, *Lemna trisulca*, *Nymphaea candida*, more rarely *Stratiotes aloides*. If the water is not too deep there appears, after the aquatic species or sometimes with them, an association of *Equisetum heleocharis*. The stems of this plant form a dense growth above water, while its rhizomes, intertwining below, give the bog plants a substratum on which they can fix themselves. Very often the colonisation by *Equisetum* is accompanied by the spreading of a moss carpet over the surface of the water, most often formed by *Hypnum aduncum* Hedw.¹ and *Sphagnum teres* Ångstr. Thus we have the two associations: *Equisetum heleocharis*-Sph. (Bystroe marsh, district of Bogorodsk, Gov. of Moscow) and *Equisetum heleocharis*-Hypnaceae (turbaries near Bisserov, district of Bogorodsk). In deeper and more peaty basins *Typha latifolia* takes the place of *Equisetum heleocharis*.

The ultimate fate of these aquatic associations is passage into the typical

¹ Kindly determined by Dr H. Paul, of Munich.

associations of the Transition bog, *Carex rostrata*-Sph. and *Carex lasiocarpa*-Sph. In the Bystroe marsh, where a little river has been absorbed by the bog, a picture of the succession of *Equisetum heleocharis* to *Carex lasiocarpa* can be observed. At the same time the floating Sphagnum covering thickens. In the middle of the former river-bed there is a dark green belt of *Equisetum heleocharis* growing on a carpet of *Sphagnum teres*. Nearer the banks the vegetation is lighter green due to *Carex lasiocarpa* and the carpet of Sphagnaceae is denser. One can easily walk across the bog on the floating Sphagnum carpet: only here and there are spaces of open water covered by aquatic plants and surrounded by *Equisetum heleocharis*. The succession is:

Nuphar luteum → { *Equisetum heleocharis* → { *Equisetum heleocharis* } → { *Carex lasiocarpa* }
Potamogeton natans → { Sphagnum } → { Sphagnum }

In the turbaries near the village of Bisserovo the succession is as follows:

Hydrocharis morsus-ranae → { *Equisetum heleo-* { *Equisetum heleocharis* } → { *Carex rostrata* }
Nymphaea candida → { charis } → { Hypnaceae } → { Hypnaceae }

The colonisation of the deeper turbaries of the Transition bogs with a layer of peat at the bottom, is simpler. The large quantity of salts in the water evidently prevents the development of aquatic plants and of *Equisetum heleocharis*, which is also hindered by the great depth of the water. Turbaries of this type are generally colonised from the sides by floating Sphagna, upon which grows *Carex rostrata*, and this *C.r.*-Sph. association covers hundreds of square metres, its development being made possible by the chemical content of the water.

EFFECT OF FIRES (see Fig. 5).

Fires are very common on Sphagnum bogs. Their effect depends upon their intensity. A great fire destroys all the vegetation and may even level the surface of a hillocky peat bog. The burn is invaded by various plants from other habitats, very often by mosses, principally *Ceratodon purpureus* (Fig. 5). The primordial vegetation re-establishes itself only very gradually.

A moderate fire dries up the surface of the bog to a certain extent and reduces the top layer of peat to ashes. Since the peat is thus enriched by mineral salts the more exacting *Betula alba* takes the place of *Pinus silvestris*. In the herbaceous layer *Eriophorum vaginatum* develops luxuriantly. The Sphagna are replaced by *Polytrichum strictum* Banks, which is constantly seen on the tussocks of the Sphagnum bog, and after a fire develops in immense quantity and fruits abundantly. The mass of its capsules on a stretch of burnt bog can be seen from a distance by their red-brown colour. This association, *B.a.-E.v.-Pol.str.*, is widely spread on burns. *Eriophorum vaginatum* in great quantity is also seen on the burns of Transition bogs.

Fires have a great influence on the life and development of the whole bog. Borders of bogs near villages are in general subject to continual fires. The

covering of *Sphagnum* almost totally disappears, the development of the bog ceases, and *Eriophorum vaginatum* and *Polytrichum strictum* permanently establish themselves.

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STUDIES ON THE ECOLOGY OF ENGLISH HEATHS

II. EARLY STAGES IN THE RECOLONISATION OF FELLED PINWOOD AT OXSHOTT HEATH AND ESHER COMMON, SURREY

BY V. S. SUMMERHAYES AND P. H. WILLIAMS.

(*With Plates II, III and ten Figures in the Text.*)

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INTRODUCTION

As mentioned in Part I (11), during the late war (November 1916–October 1917) a considerable portion of the older part of the pinewood at Oxshott Heath and Esher Common was felled. Since then recolonisation has been proceeding actively making it in many respects the most interesting part of the Common. Our first visit being in October 1920, the account is in some ways incomplete, but we have been enabled to add to it by the kindness of people who had visited the Common in the interim. In addition the extensive fires in 1921 rendered nugatory much of the colonisation prior to that date; thus the process was delayed and we were able, so to speak, to gain time. Although the succession on the felled area has reached only a comparatively early stage, yet we feel that the position is of sufficient interest and affords enough material to justify description now. It was hoped to follow the progress of recolonisation and to publish further accounts at such future times as might seem proper, but unfortunately the authorities have now decided to replant the area at an early date so that it will not be possible to complete our observations. Indeed a small area was planted with pines during the spring of 1925, but the interference with the natural course of events has not yet been very considerable. In spite of this sudden termination to the work it still seems of value to publish the observations, etc., already made, and we hope that we may be able to follow the later phases elsewhere.

Much of the earlier work embodied in this account was done in conjunction with the late Mr L. W. Cole whose many helpful suggestions and indefatigable industry have contributed greatly to the completion of the work. Mr Paul Richards has been studying the Bryophytes and Lichens of the commons during the past two years, and has kindly supplied us with much information with respect to the ecology of these groups. We should also like to express our thanks to Messrs Somerville Hastings, W. J. Lucas and R. Paulson for information about the condition of the Common prior to felling and from that time until 1920; to Mr R. E. Hunter for help in some of the surveying; and to the British Rainfall Organisation for the rainfall data given.

An examination of the map in Part I (11, p. 289) will show that the felled area occupies the northern half of the Common, including the whole of the North Ridge and the northern and central valleys. It forms a continuous stretch with the exception of the large isolated circular felled region ("Inner Circle") just north of Sandy Lane which is separated from the main felled area by a narrow strip of pines. To the east, just north of Copsen Farm, the felled region adjoins the original heathland of Round Hill and vicinity; elsewhere it is bordered by woodland or wooded parkland.

The pinewood in the felled part was considerably older (60–90 years of age) at the time of felling than the part now standing, this being probably the explanation of the partial felling. The felling was somewhat irregular, as

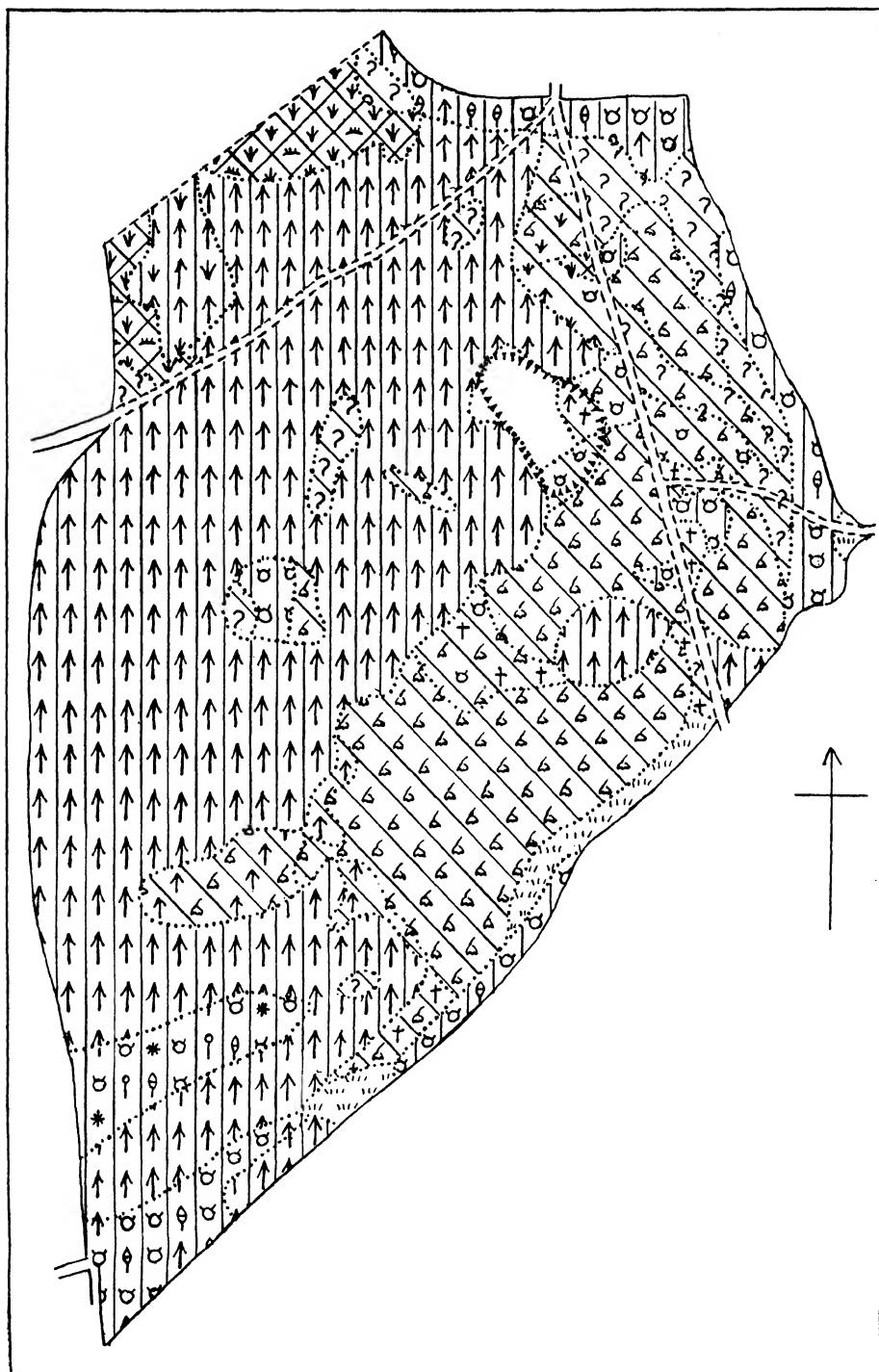


FIG. 2. Vegetation map of southern part of Oxshott Heath. Scale and symbols as in FIG. 1.

can be seen from the map (see Part I), for while the older trees were generally completely removed yet clumps of trees, marginal strips and isolated specimens were left in places. The conditions in the pinewood before felling are unfortunately unknown to us personally, but from verbal accounts the wood generally resembled the part still standing. The higher parts had no ground vegetation at all in most places. On much of the damper ground stunted tufts of *Molinia* had survived since the pine colonisation some 60 to 70 years previously. There were bog areas along the valley crossing the "neck" north of Sandy Lane, just north of the Great Plantation and around Black Pond, there being a well-developed Juncetum at the eastern end of the latter. The most striking change since felling has been the great extension of the wet-type communities. It was the conversion of a dry woodland into bog communities subsequent to felling that first drew our attention to the region.

A detailed survey of the vegetation of the Common was made on a scale of 12 ins. to 1 mile in the early part of 1921 and the results are given on the accompanying maps (Figs. 1 and 2). On the map the outlines of all the principal communities are traced and the state of colonisation of the felled areas at that time can be easily seen.

The mode of representation of the vegetation follows in all but a few details the scheme outlined by Salisbury in this JOURNAL, 8, No. 1, 1920, pp. 60-61. This scheme has been found quite satisfactory, the basis and species symbols being employed with certain modifications. Two new species symbols have been introduced for *Castanea sativa* and *Epilobium angustifolium* respectively. The area to be mapped here, however, is in a state of rapid succession so that it was necessary to introduce a few new types of representation. Such for instance is the method of representing the invasion of a Molinietum by birch scrub: another example is the variable spacing of the species symbols to denote different degrees of openness in the plant covering. The point at which a moorland community with scrub is converted cartographically into scrub with the woodland basis symbol is naturally arbitrary but corresponds roughly with a continuous scrub 6 ft. in height. "Birch Heath" is used on this map to denote heathy parts with young birches dominant or co-dominant and not for places where the birches are full-grown, which are included in "Mixed Wood" (see Part I). It was decided also to put in "Grass Heath" under the grassland basis symbol rather than class it as a type of heath.

It may also be mentioned that the distances between the basis symbol lines were originally just over 0.2 inch (5 mm.), this being found convenient since it gives ample room in which to draw the species symbols.

1. COMMUNITIES ARISING AFTER FELLING

The communities resulting from recolonisation can be divided into two series, viz. Dry Series and Damp Series. These two are not always clearly separable, there being quite wide transitional zones in places in which the

dominants of the two series are in competition, and which in other respects show special features.

A. DRY SERIES.

These are communities developing on the higher and drier parts of the felled areas where water does not lie at all during the winter. From Fig. 1 it can be seen that the dry areas form a continuous zone across the centre of the felled region. On felling a large region almost bare of vegetation was produced and on this area, owing to its exposed position, especially along the North Ridge, the surface soil rapidly dried out. On the crest itself the wind soon removed the needle covering, but on the lower slopes this was retained and exerted a very important influence on the developing vegetation. This acid litter and peat is very unfavourable for plant life as the surface dries out almost completely in dry weather, with the result that colonisation was very slow until the surface layer became decomposed more completely. At this point, however, another adverse factor came into play, namely, the formation of "surface scale." Farrow (4, p. 149) has noticed the unfavourable effect of surface scale on colonisation. At Oxshott a thin layer (half an inch = 1.25 cm.) of semi-decomposed pine litter tends to dry up and shear away from the soil beneath in dry weather, particularly around pine stumps. Any seeds falling on this area and germinating after rain would find themselves cut off from below with a considerable crack to traverse and would die of drought if dry weather supervened. It was observed in 1923 that more *Calluna* seedlings appeared where no "scale" existed or where the surface was almost pure sand. Where seedlings were found in "scale" areas they were almost invariably associated with the vertical cracks in the surface layer. That the actual nature of the peat at this stage was not inhibitive *per se* was shown by the fact that in places many *Calluna* seedlings occurred where the surface was pure powdery peat. As a result of these various factors colonisation was postponed in many places until the peat layer was almost completely denuded. The delaying effect of the undecomposed humus-layer is still well shown on some of the lower ridges where a combination of good drainage and comparative protection from wind has prevented the rapid removal of the peat.

(I) *The Pioneer Phase.*

A number of pioneer communities have been developing on the dry areas since the felling, most of them being dominated by a single species. The following plants have formed such communities in varying degrees: *Pteridium aquilinum*, *Calluna vulgaris*, *Epilobium angustifolium* and *Betula* spp. (*B. alba* and *B. pubescens*). These species did not all start equal in the competition for the new ground: *Pteridium* was already present as communities in the pinewood, *Calluna* occurred as isolated individuals in the body of the wood or as larger patches in openings, while both *Betula* and *Epilobium* have had

to migrate from outside. These differences have played a large part in determining the course of recolonisation.

After felling the first development of the plants in the drier regions was the recovery of *Pteridium* and isolated Ericaceous shrubs. The degree to which the latter had survived in the older pinewood is not known, but in view of the greater age of this part of the wood compared with the existing part it seems likely that they had done so in very favourable spots only. There are however several places where the pines had apparently never reached any great size, and there heath vegetation persisted.

(a) *PTERIDIUM AQUILINUM* CONSOCIATES.

Pteridium, which spreads by rhizome growth only in these dry regions, forms communities very similar to those described in Part I. The districts covered by *Pteridium* at present are in all probability the same as those occupied in the original wood, although increase in area has taken place. As far as we are aware, no new *Pteridium* communities have originated in the dry regions since 1920. Sharp edges to the bracken communities such as described for Breckland (2, p. 223) have been noticed, and are well marked where the *Pteridium* is advancing over almost bare, fairly uniform slopes or flats. Except against one plant *Pteridium* has had little opportunity of making use of its well-known power of competition, owing to lack of organised competitors. The exception is *Epilobium angustifolium* which quite early had covered extensive stretches of ground on the northern ridge. Here it is being invaded by *Pteridium*, the border line between the two communities being sharply defined. On examining the *Pteridium* numerous plants of *Epilobium* were found among it. Owing to its great height *Epilobium* is not so easily ousted by *Pteridium* by shade effect as other plants are. The flowering stems grow above the bracken and are thus in open daylight, but the shorter sterile stems and all the stems in the earlier stages are badly affected by the shading of the bracken. Although *Epilobium* sprouts before *Pteridium*, the latter soon overtakes it so that until the *Epilobium* shoots push through the curtain of fronds, they are in considerable shade. It is probable, however, that the reduction in nitrification correlated with the increase in acidity of the soil under *Pteridium* has a greater effect than the shading. *Epilobium* is a "nitrate-loving" plant (7, résumé, p. xliii), the luxuriance of its growth being more or less directly related to the nitrifying power of the soil, and estimations have shown that nitrification is less active under *Pteridium* than among the *Epilobium* outside the bracken community. Thus the willow herb will be gradually replaced by the bracken. This process is being followed in greater detail by means of selected quadrats.

Apart from *Epilobium* the *Pteridium* communities are remarkably pure, especially in the older parts where the action of the fronds has been continuous

over a longer period, except for young birches of all sizes which are to be found growing among the bracken.

Only a small portion of the higher ground is occupied by *Pteridium*, the remainder being the scene of struggles between other plants. We would wish to emphasise that all the dominant plants and most of the others as well are able directly to colonise the bare ground. It is first necessary that the pine litter should be partially decomposed by soil fungi and bacteria before the higher plants can obtain a foothold, but lower plants other than these play no necessary rôle as prime colonisers.

(b) *CALLUNA VULGARIS* CONSOCIES.

The coloniser *par excellence* of the dry regions of the felled area is, as might be expected, the heather, *Calluna vulgaris*. Since the original Callunetum is on the far side of the unfelled pinewood very little help has come from that source; this explains the tardiness of the spread of *Calluna* at first. It was not until the surviving plants in the larger openings in the wood, or perhaps in the body of the wood itself, had recovered sufficiently to flower and produce the seed necessary for colonisation that any rapid spread took place: also it is probable that the pine-needle covering was at first not sufficiently decomposed. At present there are many plants which produce prodigious quantities of seed. The heather grows very quickly on such soil and is rapidly producing a continuous, if low, carpet of vegetation. The favourable conditions for growth are well exemplified in the very profuse flowering which in its turn produces more seed and fresh plants. The two photographs (Plate II, figs. 1 and 2) show the same view taken in 1922 and 1925 respectively.

Although in many places the new Callunetum is thick and from 9–12 ins. high, there is as yet little of the ground vegetation found in it elsewhere (cf. Part I). The mosses *Campylopus flexuosus*, *Webera nutans*, *Polytrichum juniperinum* and *P. formosum* are present in very small quantity under the heather: continued search failed to discover either *Hypnum cupressiforme* var. *ericetorum* or *Dicranum scoparium*, which are so frequent in the mature Calluneta. The first named is doubtless handicapped by its rare fruiting whereas *Polytrichum* fruits regularly so that the spores soon reach the newly covered areas. There are a number of localities on the felled areas where the presence of small pine trees up to 20 ft. in height and the absence of large stumps indicate the former presence of an opening in the mature wood. Here the typical Callunetum mosses mentioned above are found although in rather small quantity. Other relict plants found on these areas include *Lecidea granulosa*, *Hypnum schreberi*, *Cladonia furcata**, *C. sylvatica*, *C. uncialis*, *C. pyxidata*, *C. fimbriata* and var. *radiata*, and *C. coccifera**. Those marked with an asterisk do not occur in the pine openings, but are ordinary Callunetum species. Very few of the above are found in the young *Calluna* consocieties.



1. Dry area in 1922 showing invasion of *Calluna* consociates. Small birches can just be detected here and there.



FIG. 2. The same area as that shown in Fig. 1, taken from the same spot in 1925, showing increase of *Calluna* and great height growth of the birches.

Observations seem to show that *Dicranum* and *Hypnum* are spreading into the *Calluna* consocieties from these relict areas.

An interesting feature in the embryonic *Calluneta* is the frequency of *Erica cinerea* (cf. 5, pp. 156-163), this plant being much favoured by the comparative lack of competition and growing very well. Its prevalence is also probably due to its greater abundance in the mature pinewood, as described in Part I. In the more closed areas *Erica* is less common. From this and other observations it seems that the explanation of the distribution of *Erica cinerea* in heath communities must be sought in its relation to *Calluna* and not in terms of habitat factors directly. It is apparent that *Erica* is always dominated by *Calluna* under normal heath conditions, in all probability owing to the latter's taller growth, but that when the conditions become abnormal *Calluna* is often affected more than *Erica*; in these cases *Erica* becomes more abundant. Such abnormal conditions are reduction of light, eating by rabbits, disturbance of soil, drying out of soil, burning of heath, etc., and it can be seen that these may have an equivalent effect in that they affect *Calluna* more adversely than they do *Erica*. Most of them are certainly unfavourable for *Erica* itself. This question is being investigated more fully.

On the ridge, which is much more exposed and has much less soil, both *Calluna* and *Erica* are less common than elsewhere. The former is gradually creeping up the southern slope and should eventually dominate the ridge, but at present (1925) *Epilobium* is the most abundant plant there. *Erica cinerea* is, however, locally abundant on certain rather dry gravelly slopes, where it forms a low interrupted sward and flowers profusely.

(c) *EPILOBIUM ANGUSTIFOLIUM* CONSOCIETIES.

One of the most interesting of the phanerogams is *Epilobium angustifolium*, since it is practically absent from the original heathland. This species was first recorded by Mr W. J. Lucas on the felled area in 1918 and apparently was absent previously since it is too conspicuous a plant to be overlooked. *Epilobium* is particularly well adapted for colonising newly-bared areas since it produces an abundance of seeds which are carried long distances by wind. In addition it has extensive branched roots usually producing a number of adventitious aerial shoots. The latter grow very closely together, and are very tall, thus being able to shade over and crowd out other plants. Our germination experiments show that usually the seeds are not able to germinate in acid raw humus, but if this is removed the plant soon establishes itself.

Until 1921 the higher ground was covered with a thick (1-3 ins. = 2.5-7.5 cm. deep) layer of partially decomposed pine-litter except at the summit of the ridge. Here the organic covering was blown away at an early date, leaving the underlying gravel, and this was rapidly colonised by *Epilobium*. In some places the effect of exposure has been so much as to remove some of

the surface soil, the pine roots being totally exposed, but the *Epilobium* has maintained itself and is still very abundant.

It has been shown (7) that the presence of *Epilobium* is closely related to the capability of the soil to produce nitrates and that nitrates are stored up in the organs of the plant, especially in the younger stages; Hesselman terms *Epilobium* a "nitratophilous" plant. In coniferous woods with a raw humus layer on the ground nitrification does not take place, but on disturbing the ground or removing the humus nitrification is initiated. Such conditions are paralleled here, the general distribution of *Epilobium* being easily explained on this basis. Soil which has been burnt always nitrifies actively for some time afterwards, and Hesselman (8, résumé, pp. ci-cv) records *Epilobium* from all such places after fires. In 1921 fires burnt away the peat completely in many places, thus enabling *Epilobium* to colonise areas where otherwise it would not have succeeded. These fires will be dealt with more fully later.

The best growth of *Epilobium* on non-burnt areas is seen in certain hollows on the northern ridge. A considerable amount of gravel has been removed producing a large depression—named by us the "Great Hollow" and described fully later on—with a number of subsidiary holes in its proximity. The sides of these pits are very steep and unstable, fragments being carried down continually from above. They may be as much as 10 ft. in depth. Hesselman (7, pp. 370–373) has described the occurrence of *Epilobium* in gravel pits in Sweden and has shown that even in quite bare mineral soils nitrification proceeds actively but is increased if humus be mixed with the gravel, etc.; such conditions are almost exactly reproduced in these hollows. Estimations of the power of nitrification of soil by the phenol-sulphonic acid method were made in one spot at the base of a slope. On testing after allowing the moist soil to stand for 25 days the soil contained 133.5 mgm. NO_3 per litre of soil. In such places *Epilobium* grows very luxuriantly, some of the shoots being over 6 ft. in height, and completely crowds out any other plants which may be present at first. It is a curious fact that in the more open parts also *Epilobium* always grows preferably in slight depressions, so that in some places where the ground is regularly ridged there are long parallel rows of plants in the grooves with quite bare ground between them. Soil samples collected from the ridges and hollows were stored for 34 days and the nitrifying power of the soil estimated. The soil on the ridges consisting of sand with a slight admixture of humus gave 0.95 mgm. NO_3 per litre of soil, while the soil from the hollows, which was a black mild humus with birch leaves, etc., gave 53.76 mgm. NO_3 per litre of soil during the same period. This shows that in the hollows the soil is a much more favourable medium for nitrification than on the ridges and in view of Hesselman's work this seems to be the explanation of the distribution of *Epilobium* in this region. Nitrification estimations in other places, however, do not always show such clear differences and no

doubt other factors enter into the problem. This is being followed up in greater detail.

The *Epilobium* consociates differs from the others mentioned in its much shorter life, as the plant rarely maintains itself for very long in any given place. This is especially so of places where burning has taken place (see later) and is no doubt due in such cases to the re-establishment of the original unfavourable conditions when certain effects of the fire have disappeared. In the areas dealt with now which are unburnt the life of the consociates is longer and perhaps in places may be indefinitely prolonged, such places being, for example, on steep banks where fresh soil is continually being exposed.

(d) ASSOCIATES OF *BETULA ALBA* AND *B. PUBESCENS*.

There are two other plants, besides those already dealt with, which form communities on the drier areas, viz. the two birches named above. Of these *B. alba* is decidedly the commoner on the dry areas; indeed *B. pubescens* is a rather rare plant there. This agrees with conditions in Epping Forest where Mr Paulson tells us that *B. alba* is more frequent on the higher and drier ground. There seems no reason for supposing that *B. pubescens* cannot grow well on dry areas since quite well-developed specimens, as healthy as any of those of *B. alba*, occur on the top of the North Ridge. Apparently it is in the seedling stage that the solution of the problem lies, plenty of seed of *B. pubescens* being available all over the heath. Unfortunately some germination experiments carried out in 1925 on the terrain in order to clear up this point were vitiated by the unseasonable drought in May and June of that year, and we have had no time to repeat the experiment. With respect to other factors we have few indications at present. Dr Salisbury suggests that *B. pubescens* grows better under more acid conditions than *B. alba*, but we can find nothing to support this at Oxshott, indeed the superficial roots of *B. alba* grow in a more acid medium in the dry *Calluna* consociates than do those of *B. pubescens* in the wet *Molinia* consociates. Mr Tansley's experience is that they grow equally well in very acid conditions, but that *B. alba* grows much better than *B. pubescens* under neutral or somewhat basic conditions, but of course we have no information bearing on that here since the lowest acidities obtained are pH 6.9.

Hybrids are very frequent at Oxshott and serve to increase the difficulty of effectively tackling the above problems; they occur occasionally on the dry areas.

As will be seen later, *Betula* colonises the damper areas more readily than the dry ones where in most places the trees are scattered at intervals of 10–50 yds. from one another. In spite of this there are several places where the birches are dominant or at least abundant. One such area is to be found N. and N.E. of Black Pond (Fig. 1). Here the ground is almost bare except for many young birches which are about 4–6 years old and up to 10 ft. (3 m.)

in height, forming a somewhat dense scrub. These birches must have colonised the bare ground here coincidentally with the *Calluna* elsewhere: they are thus true pioneer colonisers.

The chief plant to be found between the young trees is *Calluna vulgaris* which is scattered about at intervals of several yards or more. On the typical developing *Calluna* consocieties it is noticeable that attack by rabbits, of which there are a number on this part, is of little importance although there is ample room for penetration between the individual plants (3, p. 61). It is only at the edges of the *Calluna* zones that the effect of rabbit attack is at all evident. It seems that there are more *Calluna* bushes than can possibly be bitten to injure them appreciably; in fact in these areas young *Ulex nanus*, *Molinia* and *Carex pilulifera* seem to be the rabbits' first choices. This is not the case in the birch area described above. Here the amount of food is strictly limited, the *Betula* being too old, with the result that almost every heather bush is nibbled down to a compact circular cushion, flowering being almost entirely suppressed. In one or two places where the *Calluna* is rather thicker it was not eaten so much and was flowering freely. The isolation of the bushes is therefore a distinctly unfavourable condition and the lack of seed production probably explains the slow colonisation of this region. It is interesting to note that isolated *Erica cinerea* bushes in the same region were practically untouched and flowering profusely. *E. cinerea* is eaten in other places on the Common, but apparently is not so much appreciated as *Calluna*; in this region there is presumably enough of the more palatable *Calluna* to satisfy the relatively few rabbits present.

The reason for the occurrence of "pioneer" birch scrub in this area is probably the close proximity of many mature trees of *Betula alba* and the consequent availability of enormous masses of seed. In most other places where the dry areas are at all near mature trees these are actually themselves in wet areas and are predominantly *B. pubescens*, which species, as mentioned above, only establishes infrequently on the drier regions. There seems to be little difference in the state of decomposition of the pine humus here and elsewhere.

(e) GENERAL OBSERVATIONS.

Scattered over the drier area and found in all the developing communities there, with the exception of those of *Pteridium*, are the following plants:

Aira praecox		<i>Molinia caerulea</i>	
<i>Betula</i> spp. (seedlings)	f.	<i>Ornithopus perpusillus</i>	
<i>Carex pilulifera</i>		<i>Pinus silvestris</i> (seedlings)	1.
<i>Cuscuta epithymum</i> (on <i>Calluna</i> ,		<i>Rubus</i> spp.	
<i>Ulex nanus</i> and <i>Erica cinerea</i>)		<i>Senecio silvaticus</i>	
<i>Deschampsia flexuosa</i>		<i>Trifolium repens</i>	
<i>Erica tetralix</i>	r.	<i>Ulex europaeus</i> (seedlings)	
<i>Fagus sylvatica</i> (seedlings) on ridge		<i>U. nanus</i>	
<i>Juncus squarrosus</i>			

In addition there are several plants usually associated with excavation heaps and rabbit burrows only.

Anagallis arvensis
Cerastium vulgatum
Cirsium arvense
Poa annua

Polygonum persicaria
Solanum nigrum
Sonchus oleraceus

The Common was used a little for military purposes during the war, and these plants were probably introduced then or during the felling; one or two (*Cerastium* and *Sonchus*) are commonly found on other parts of the heath and are, no doubt, constant immigrants from outside.

Among the plants of the first list there are some which offer points of interest. *Erica tetralix* and *Molinia* are found almost exclusively in the zones bordering on the wet series of communities. The latter in particular seems to be extending its range rapidly upwards on the higher ground. Isolated tussocks far from the main body of *Molinia* are thriving and have produced inflorescences up to 3 ft. in height during the past three summers. In these cases however the tussocks were growing apart from *Calluna*, *Molinia* probably not being able to compete successfully with *Calluna* in these dry districts. As mentioned above, *Molinia*, when growing isolated, also suffers from the attack of rabbits. On quite dry ridges small *Molinia* tussocks are found bitten right to the ground and this is, no doubt, a potent factor in preventing the spread of *Molinia* above a certain contour.

Ulex nanus has appeared, chiefly in the *Calluna* areas, where it is growing well in many places, producing upright and oblique shoots and flowering. In the shelter of birches it forms large bushes about 3 ft. high. In the barer parts it is early attacked by rabbits which keep on nibbling away the soft young shoots and thus keep it in close cushions. Fritsch and Salisbury (6, p. 135) note the rarity of establishment of seedlings at Hindhead and this corresponds with the slow spread at Oxshott since all the plants must have come from seed. *U. europaeus* seedlings are growing in several spots in the bare areas especially near Round Hill where the plant is common on original heathland.

Cuscuta occurred very abundantly both in 1922 and 1923, but less frequently in 1924 on the young *Calluna* bushes. It was also seen on *Erica cinerea* and *Ulex nanus*. In 1922 it did a considerable amount of damage to the bushes, but in 1923 the attack was not so severe. Although cases have been noted in which plants have died after an attack by *Cuscuta*, yet generally the damage is not so great and is usually limited to a complete or partial prevention of growth in size. Some plants seem to be attacked more or less regularly every year, others only occasionally.

Senecio silvaticus is a very characteristic plant of the partly bare regions where it often occurs in large clumps. It seems to prefer those places where the humus covering is thinner or absent, such as the vicinity of rabbit burrows. Apparently it is a "nitratophilous" plant like *Epilobium angustifolium* (7, résumé, p. xliii) and only occurs where nitrification is active in the soil. Its occurrence at Oxshott in similar places to those occupied by *Epilobium* is

therefore easily explained. It was first recorded in 1918 and has spread very considerably between 1922 and 1923, doubtless owing to its efficient means of dispersal. On the ridge it is restricted to depressions, probably because the seeds are all blown into the hollows, since in some of its stations lower down it is almost as much exposed to desiccation in the seedling stage; the explanation may perhaps be similar to that given above for *Epilobium*. *Senecio* is mainly a biennial plant, many seedlings appearing in the autumn of the year previous to flowering, but it may also be an annual. This, together with its relatively short flowering period and its lack of means of vegetative spread, renders it a much less efficient coloniser than *Epilobium*.

The species of *Rubus* occur in the form of low bushes which spread by means of creeping stolons in all directions. Several species are included in this category, but as no difference in procedure was noticed they are treated together.

In order to test the effectiveness of these stolons as a means of colonisation measurements were made from a number of these bushes. It was found that in February and March 1923 most of the plants had at least one stolon rooted, although the majority of the stolons were not. The following are distances from the root of the main plant at which stolons were found rooting:

Plant 1. 8 ft. 3 in.

Plant 2. 8 ft. 8 in. (to N.E.), 8 ft. 7 in. (to S.), 6 ft. 6 in. (to S.), 6 ft. 0 in. (to N.W.).

Plant 3. 9 ft. 5 in. (to W.), 7 ft. 6 in. two stolons (to N.).

It must be remembered that the actual lengths of the stolons were often greater as they do not always grow straight. In Plant 2 an unrooted stolon had reached the length of 14 ft. 5 in. (4.4 m.), while a young plant which had obviously originated from the older one was found 7 ft. 4 in. from the parent.

The area of Plant 2 was re-examined in the spring of 1925 and it was found that the two bushes recorded in 1923 had been converted into a large number of closely placed plants which are gradually matting together into a low tangle. The lengths of the stolons were again measured, the longest one found rooting being 10 ft. 10 in. (= 3.25 m.), while there were non-rooting stolons up to 13 ft. 2 in. in length. Both in 1923 and 1925 the majority of the stolons had rooted in heather bushes, although in 1925 a case was seen in which a stolon branched at the tip had rooted in several distinct places, all in the open, but one of them had actually forced its way between the bark and wood of a pine stump. However in most cases the stolons terminating in the open seemed incapable of rooting, possibly owing to animal attack or frost. The old stolons only maintain connection between parent and offspring for three years at the most—they are dead the last year—and after that time it is difficult to decide from what source a young plant has been derived.

It will be seen from the Plant 2 figures above that young plants may be produced in many directions at once: obviously *Rubus* is quite capable of

increasing rapidly in favourable localities. The seeds are presumably bird-dispersed in the first place; the species is thus being recruited continually from elsewhere. The plants themselves flowered and fruited in the summers of 1923 and 1924, and there is every reason for believing that many new ones have arisen by seed from the others nearby. It is noticeable here, as on the unfelled heath, that the bushes are commonest in the vicinity of rabbit burrows. This is doubtless due to the disturbance of the ground and removal of the unfavourable humus layer (cf. Part I, p. 294).

Where all the humus has been removed on the ridge by wind a hard rock-like surface of sand is often left. This is almost impossible to colonise except by vegetative growth from more favourable centres on the part of plants like *Epilobium* and *Pteridium*; it is therefore almost completely bare.

The following mosses occur on the drier felled areas, viz. *Bryum argenteum*, *Funaria hygrometrica*, *Polytrichum juniperinum*, *P. piliferum*, *P. formosum*, *Dicranum scoparium* and *Webera nutans*. None of these is at all common except on burnt ground. Under isolated birch trees or groups of trees thin carpets of the above mosses are sometimes found. On this moist substratum the large lichens *Peltigera spuria* and *Cladonia pyxidata* occur occasionally. The lichen *Lecidea uliginosa* occurs commonly on the peat in much of the drier region, especially in the *Calluna* zone. It is often the first coloniser in such places and seems to be an important factor in the production of surface "scale" owing to the binding action of the hyphae on the surface layer. Another lichen occurring in similar places, but by no means as commonly, is *Cladonia uncialis*; this however plays no part in the formation of surface scale. *Lecidea granulosa* also is found, rarely, in the *Calluna* consocieties. Considered generally, the lower plants do not act as prime colonisers at Oxshott.

(II) *The Birch Phase.*

In addition to the pioneer communities of *Betula* described above there are seedlings and young trees of both species to be found everywhere, though never abundantly. These trees grow among the *Calluna* and *Epilobium* and more rarely in the Pteridietum. They are most frequent where the vegetation is sparser and do not seem to be able to invade the closed communities very easily. We may consider these to be the vanguard of the "Birch Heath" phase in the succession, but it is very difficult to say to what extent this phase will become established on the dry areas. In a few places, especially among *Epilobium*, the birch has grown so compactly as to produce open scrub, and in one or two places in slight depressions small birch thickets are found. The best example of the Birch Phase is to be found in the Great Hollow, and for this reason among others we give a more detailed account of it.

The Great Hollow. On the northern slope of the ridge is a large hollow which was probably first formed by digging for the gravel there. It dates from pre-pine-wood times, as large pine stumps (90 years old) occur at its

bottom. The depression is about 100 yds. (90 m.) long, is in some places 20 ft. (6 m.) deep and has very precipitous sides except towards the north. The "Great Hollow," as we have termed it, is interesting because it shows the effect of protection on the nature and rate of colonisation of the felled regions. It is probable, judging from the ages and spacing of the felled trees that there was no more vegetation originally in the hollow than elsewhere, but now there is a very striking difference, the vegetation being very rich and varied, while the slopes outside are much barer.

The dominant vegetation consists of a scrub with large numbers of the two birches, *Betula alba* being much the commoner, and young trees of *Pinus*. In the spring (February) of 1923 the pines were mostly from 2 ft. 6 in. (76 cm.) to 4 ft. 6 in. (137 cm.) high, and were very close together in many places. The birches were rather taller, being up to 8 ft. (2.64 m.) in height on the same date, but a number of the tallest birches had been felled in the summer of 1922 so that really the birches were still further ahead. Where *Pinus* occurred in quantity *Betula* was not common.

In view of the question of succession from *Betula* to *Pinus* some measurements were made to see what were the annual increments in the lengths of the leading shoots of the two species at 1922 were age gains in a year. With *Pinus*, at the eastern end, the increments were from 26-45 cm., an average percentage increase of 54.7, and in the centre in rather smaller trees the increments were 18-38 cm., an average of 40 per cent. *Betula* at the eastern end with increments of 60-115 cm., had an average increase of 71.5 per cent. These and the *Pinus* were of approximately equal ages (3-5 years). From the bases of the large birches felled in 1922 shoots of 166-193 cm. had developed. It can be seen that the growth of *Betula* is extraordinarily rapid, so that it will at first outstrip *Pinus*. This is in accordance with other accounts.

In early 1925 the ascendancy of the birches was very marked, the largest being up to 12 ft. or about 4 m. in height, in places forming an almost impenetrable thicket, but later in the year these were nearly all felled in connection with the replanting mentioned above. It was very noticeable how the social habit of the young pines completely prevented the growth of the birch locally.

Growing among the young trees and on the bottom of the Great Hollow generally is a well-developed carpet of *Calluna* and *Erica cinerea*. Around the edges, especially where the slope is steep, *Epilobium angustifolium* flourishes while *Pteridium* is dominant in a few places. The following is a general list for the Hollow made in 1922:

<i>Betula alba</i> (young)	a.—l.d.	<i>Q. sessiliflora</i> (young)	o.
<i>B. pubescens</i> (young)	o.—f.	<i>Rubus idaeus</i>	1 plant
<i>Castanea sativa</i> (young)	o.	<i>R. fruticosus</i> agg.	o.
<i>Fagus sylvatica</i> (young)	r.	<i>Salix cinerea</i>	r.
<i>Pinus silvestris</i> (young)	l.d.	<i>Sorbus aucuparia</i> (young)	r.
<i>Quercus cerris</i> (young)	r.	<i>Ulex europaeus</i> and seedlings	o.
<i>Q. robur</i> (young)	o.		

<i>Calluna vulgaris</i>	f.—a.	<i>J. squarrosus</i>	r.
<i>Carex pilulifera</i>	f.	<i>Lotus uliginosus</i>	r.
<i>Deschampsia flexuosa</i>	o.	<i>Molinia caerulea</i>	r.
<i>Digitalis purpurea</i>	r.	<i>Ornithopus perpusillus</i>	r.
<i>Epilobium angustifolium</i>	l.a.	<i>Potentilla erecta</i>	r.
<i>Erica cinerea</i>	a.	<i>Pteridium aquilinum</i>	o.—l.a.
<i>E. tetralix</i>	r.	<i>Rumex acetosella</i>	r.
<i>Galium saxatile</i>	r.	<i>Senecio jacobaea</i>	r.
<i>Hieracium pilosella</i>	r.	<i>S. silvaticus</i>	r.
<i>H. umbellatum</i>	l.f.	<i>Veronica officinalis</i>	r.
<i>Juncus effusus</i>	o.		

Most of the plants were present only in very small numbers, as is quite evident from the lists. This is probably due to the time factor: they have not had time to get there yet in quantity. The majority of the typical heath plants are included in the above list and it is doubtful whether the list will be enlarged much in the future especially as the pines are growing rapidly. At present (1925) the list is quite complete; in fact several of the above species cannot now be found in the Hollow. The wholesale destruction of *Calluna* bushes by the shade of the closely placed birches was a striking feature noticeable on felling. There are one or two deeper hollows where water lies during the winter; it is here that the damp-loving types are found. In a general way it may be considered that the Great Hollow probably represents a stage of colonisation which will not be reached on the other parts of the dry areas for some years to come and is in that connection of especial interest.

(III) *The Pine Phase.*

The above facts are particularly important in relation to the "Pine phase" which one would naturally expect to follow the "Birch phase," but in the Great Hollow the succession has been telescoped and the pines have appeared very early. In this area, in addition to the sheltered conditions in the Hollow, an important factor is the presence of a clump of unfelled pines just near. These have sown seed since 1917 and there are numerous young pines on the north slopes of the ridge around the clump. Also on the very crest young stunted fasciated pines are found, although there the conditions are not at all favourable for the establishment of *Pinus*, the soil being bare and stony. Elsewhere on the dry areas young pines are very infrequent; it is probable that the critical point is at the development of the first foliage leaves or perhaps even earlier. In the course of some experiments in which pine litter from the pinewood was placed on certain areas, a number of pine seeds germinated, but all the seedlings died away some time after the above-mentioned stage although at first they looked quite healthy. In most of the region in July, when *Pinus* germinates, the higher exposed ground is usually very dry and not favourable. Perhaps with the increase in the plant covering now taking place *Pinus* will find more advantageous conditions. The observations given above, however, seem to show that the lack of seed supply is a very important and perhaps the deciding factor.

(IV) General Remarks.

The scheme of colonisation on the drier parts of the felled areas may therefore be represented as follows, the double lines indicating the more important lines of development (see Fig. 3). What follows *Epilobium* seems to be largely a matter of chance since apparently it is not capable of remaining indefinitely in a region, but rather depends on colonisation of new areas for its success. It is therefore replaced by various plants according to different circumstances.

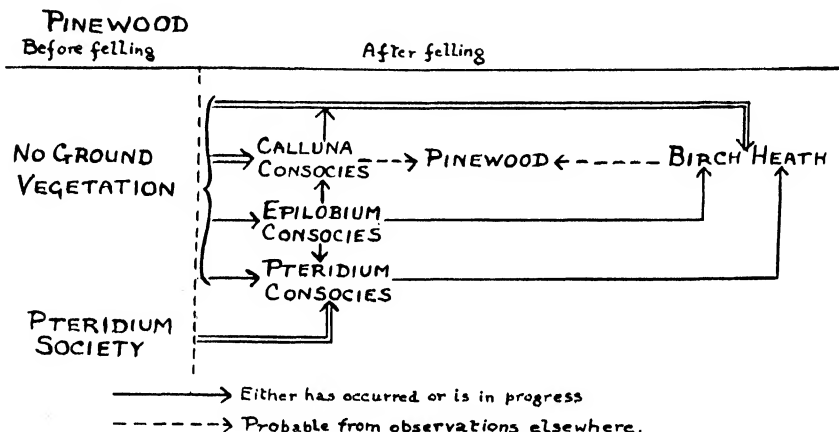


FIG. 3. Scheme of colonisation of the dry areas. Double lines indicate the more important lines of succession both in this and in later diagrams.

It is very interesting to note that young seedlings of *Betula* can establish themselves in *Pteridietum* of moderate thickness, a fact which had been suspected previously on the unfelled areas, but it is doubtful if colonisation of really luxuriant *Pteridietum* ever takes place. It is an important point that according to our observations the thickness of the bracken in a given place fluctuates, possibly due to the temporary accumulation of autotoxins and thus during the period of minimum thickness the birch may get established. Afterwards its very rapid growth enables it to compete with the *Pteridium* for light.

Information as to some of the later stages of the above scheme is of course lacking, so we can only make suggestions as a result of observations on the original heathland and from other heaths.

B. DAMP SERIES.

On the lower and wetter parts of the felled area the progress of recolonisation is quite different from that already described, the dominant plants here being *Molinia*, various species of *Juncus* (*J. effusus* and *J. conglomeratus* in particular) and *Betula* spp. Partly owing to the greater water-content leading to more favourable conditions generally, and partly to the presence of *Molinia*

in the original pinewood, the colonisation has proceeded more rapidly and would be at a much more advanced stage still were it not for the disastrous fires of 1921.

In the lower regions the soil is in many respects different from that on the higher parts. In all cases there was still a considerable peat layer on the surface and although much of this has been removed by the fires yet in no place has the humus been entirely blown away as on the ridge. Again, owing to the greater initial and subsequent water contents the pine-humus has decayed more rapidly than on the drier areas, giving place to less acid peat layers of *Molinia*, etc., while surface scale is entirely unknown. The almost continuous moist condition of the surface layers also allows of more effective germination and establishment. All over the relatively unburnt regions—scarcely any of the lower part of the heath was entirely untouched by the 1921 fires—there is now a peaty layer one or more inches (over 2.5 cm.) in thickness while in places where there were bogs in the original pinewood the peat is somewhat thicker. The drainage in large areas of the low-lying parts has, since 1920 at least, been very defective in spite of the numerous drains cut, there being many large pools of water which are more or less permanent throughout the winter.

Another point of interest which is of importance in its bearing on the later stages in the succession is the fact that the damp areas are peripheral to the felled region and thus in close contact with unfelled woodland around. As a result of this many more disseminules fall on the damper parts than on the dry ones. The total result of all the factors mentioned above is the much more rapid colonisation of the damp areas as already stated.

(I) *Primary Communities.*

There are no true pioneer communities on this part of the Common as the soil was already occupied by some sort of ground vegetation previous to felling. *Molinia* was present in a very stunted condition over most of the damper parts of the wood and on felling this rapidly sprouted anew, forming a coarse herbage in 1918. By 1920 the *Molinia* herbage had been transformed into a tall tussock grassland with innumerable inflorescences.

Perhaps the most striking feature of the felled areas in early 1921 was the great stretches partially or wholly dominated by *Molinia caerulea*. This is evident from the map (Fig. 1). It is useful to note that the boundary of the *Molinia* consociates marks the upper limit of the damp type communities in practically all parts, corresponding usually to a definite contour on the terrain. However, where there are broad transitional regions the delimitation of damp and dry series is difficult. Unfortunately the fires in 1921 interfered greatly with the course of colonisation. In many places a quite new succession has been initiated following these fires; this will be dealt with later. Over a great deal of the ground, however, the burning was not severe enough to

exterminate the dominants, which have recovered again: probably the succession here, although delayed several years, is in the main not much altered.

The primary communities can be divided into several types which are on the whole related to the drainage; other factors also enter the arena in places and cause modifications. In this "water-content series," passing from the driest to the wettest, one finds (a) *Molinia* consociates, (b) *Molinia-Juncus* ecotone, (c) *Juncus* associates. In addition to these are areas with *Sphagnum* sub-dominant on the site of old bogs in the pinewood and better considered as a relict community (d).

Immediately below the dry series or transitional communities (see below) *Molinia* occurs, with some *Calluna* and *Erica tetralix*, and then gradually *Juncus* appears more and more abundantly, until at the lowest levels almost pure communities of *Juncus* occupy the ground.

At an early stage in the development of these communities seedlings of *Betula* appeared, but it was some time before the birch phase was reached in most areas. This topic will be dealt with later. Nevertheless isolated trees or small clumps were scattered throughout the dominant *Molinia* or *Juncus*.

(a) *MOLINIA* CONSOCIATES.

In 1920-1922 this community covered large stretches in the centre of the lower parts of the Common, where the ground was most free from colonisation by the birch. Apart from the young trees the community was strikingly uniform in appearance, consisting of large tussocks growing close together and producing inflorescences up to 3 ft. 6 in. (1 m.) high. Around the pine-stumps, where there was a thicker layer of organic material, there were often considerable bare spaces, but otherwise the vegetation was closed. The chief associates of the *Molinia* were *Calluna* and *Erica tetralix*, the latter being especially abundant locally, while *Calluna* was commoner nearer the upper edge of the community. Since 1920 these two species have increased greatly on the drier upper levels: this rather supports the suggestion made in Part I (11, p. 295) that pure *Molinia* communities are rarely found on such heaths, the mixed type of community being more frequent. It is probable, at any rate we know no example to the contrary, that permanent Molinieta do not exist on heaths in the low rainfall districts of England. Where the drainage is good the *Molinia* is replaced by other herbaceous or dwarf-shrub species, while on damper soils woodland is soon established. *Molinia* communities therefore only appear as a stage in succession after felling or perhaps burning. *Juncus effusus* is frequently found along lines of drainage and represents outliers of the wetter type communities.

On the lower levels species of *Juncus*, and damp-loving forms in general, are much commoner, although *Molinia* is still usually dominant. Water often lies about in pools during the winter, and soil analyses show that, allowing

for organic matter, the water-content is on the whole rather high even where spots are chosen away from large clumps of *Juncus*. In one place in this zone among almost pure *Molinia* the water-content two days after rain in March 1922 was 423 per cent. of the dry weight in the surface peat layer—this soil did not appear at all wet—and figures between 150 and 200 per cent. are not infrequent. In summer the area is drier, but the average water-content of the sub-peat layer is then about 25-30 per cent. of the dry weight.

Subjoined is a general list of species for the *Molinia* consocieties, made in June 1922, but it must be remembered that the fires of 1921 in all probability exterminated the rarer species.

Young trees and shrubs.

<i>Betula alba</i>	o.—f.	<i>Sorbus aucuparia</i>	r.
<i>B. pubescens</i>	f.—a.	<i>Rhododendron</i> sp.	v.r.
<i>Castanea sativa</i>	o.	<i>Rubus fruticosus</i> agg.	o.
<i>Ilex aquifolium</i>	v.r.	<i>Salix cinerea</i>	o.
<i>Pinus silvestris</i>	o.	<i>Ulex europaeus</i> and seedlings	r.—o.
<i>Populus alba</i>	r.	<i>Quercus robur</i>	o.—f.

Dwarf shrubs and herbs.

<i>Agrostis alba</i>	o.	<i>E. tetralix</i>	f.—l.a.
<i>Anthoxanthum odoratum</i>	o.	<i>Eriophorum angustifolium</i>	r.
<i>Calluna vulgaris</i>	o.—l.a.	<i>Holcus lanatus</i>	r.—f.
<i>Carex binervis</i>	o.—l.f.	<i>Hypochaeris radicata</i>	o.
<i>C. goodenowii</i>	o.	<i>Juncus acutiflorus</i>	r.
<i>C. hirta</i>	r.	<i>J. bufonius</i>	o.
<i>C. muricata</i>	r.	<i>J. conglomeratus</i>	o.—f.
<i>C. pilulifera</i>	r.	<i>J. effusus</i>	r.—l.a.
<i>C. stellulata</i>	r.	<i>J. squarrosus</i>	o.—f.
<i>C. vulpina</i>	r.	<i>J. supinus</i>	o.—f.
<i>Cirsium arvense</i>	r.	<i>Lotus uliginosus</i>	r.—o.
<i>Cuscuta epithymum</i> (on <i>Calluna</i>)	l.	<i>Luzula congesta</i>	o.
<i>Deschampsia flexuosa</i>	r.	<i>L. multiflora</i>	o.—l.f.
<i>Drosera longifolia</i>	v.r.	<i>Molinia caerulea</i>	d.
<i>Eleocharis palustris</i>	r.	<i>Potentilla erecta</i>	o.—l.f.
<i>Epilobium angustifolium</i>	r.	<i>Pteridium aquilinum</i>	o.
<i>E. hirsutum</i>	r.	<i>Polygonum hydropiper</i>	r.
<i>E. montanum</i>	o.	<i>Rumex acetosa</i>	l.
<i>E. palustre</i>	o.	<i>R. crispus</i>	r.
<i>E. tetragonum</i>	o.—f.	<i>Scirpus caespitosus</i>	r.
<i>Erica cinerea</i>	v.r.—r.	<i>Teucrium scorodonia</i>	r.

It will be noticed that most of the above species are far from common; indeed they rarely affect the uniform appearance of the *Molinia*.

With the phanerogams in the *Molinia* consocieties grow a number of bryophytes, some of which may be considered as relict from the pinewood, while others have probably come in since felling. None of them is very common although some can usually be found under the *Molinia*, etc.

<i>Catharina undulata</i>	<i>Leucobryum glaucum</i>
<i>Ceratodon purpureus</i>	<i>Marchantia polymorpha</i>
<i>Dicranella heteromalla</i>	<i>Mnium hornum</i>
<i>Dicranum scoparium</i>	<i>Polytrichum commune</i>
<i>Hypnum cupressiforme</i>	<i>P. juniperinum</i>
var. <i>ericetorum</i>	<i>Webera nutans</i>
<i>Lophocolea cuspidata</i>	

Hypnum ericetorum probably survived from the pinewood in the shelter of *Molinia*: it will be remembered that it does not occur on the drier parts; it was probably killed after felling by exposure on the dry bare ground.

(b) *MOLINIA-JUNCUS* ECOTONE.

This occupies a belt of varying width between the drier *Molinia* and the wetter *Juncus*, the two plants being usually in equal quantities: *Juncus effusus* and *J. conglomeratus* are the two most important rushes. The community is typically developed where the water content of the soil is relatively high but the drainage is fairly good, as along the larger drains. The associated flora is intermediate between that of the *Molinia* consocieties and the *Juncus* associates, damp-loving species having higher frequencies than those given in the above list. There are also a few additional species, viz. *Cirsium palustre*, *Hydrocotyle vulgaris*, *Viola palustris* and *Scutellaria minor*.

The following is a list of the plants found in the *Molinia-Juncus* ecotone.

<i>Agrostis alba</i>	a.	<i>J. effusus</i>	f.—c.d.
<i>Anthoxanthum odoratum</i>	o.	<i>Lotus uliginosus</i>	f.
<i>Athyrium filix-foemina</i>	r.	<i>Luzula congesta</i>	o.
<i>Calluna vulgaris</i>	o.	<i>L. multiflora</i>	o.
<i>Cirsium palustre</i>	f.	<i>Molinia caerulea</i>	a.—c.d.
<i>Dactylis glomerata</i>	r.	<i>Myosotis caespitosus</i>	l.
<i>Epilobium angustifolium</i>	r.	<i>Potentilla erecta</i>	f.
<i>E. palustre</i>	o.	<i>Ranunculus flammula</i>	r.
<i>Erica tetralix</i>	f.	<i>R. repens</i>	l.f.
<i>Hieracium umbellatum</i>	r.	<i>Scabiosa succisa</i>	o.
<i>Holcus lanatus</i>	f.—l.a.	<i>Scrophularia aquatica</i>	r.
<i>Hypericum pulchrum</i>	r.	<i>Scutellaria minor</i>	o.—l.f.
<i>Juncus conglomeratus</i>	f.—a.	<i>Viola palustris</i>	o.

(c) *JUNCUS* ASSOCIATES.

Juncus was very rare in the wood before felling, being nearly restricted to the environs of Black Pond. Possibly the series of communities mentioned above represents different stages in the invasion of the *Molinia* consocieties, which had a start in the race after felling, by species of *Juncus*. It seems probable, however, that complete replacement of the *Molinia* will not take place at the higher levels, even if it does elsewhere. Burnt patches in this region have been filled in some places with numerous *Juncus effusus* seedlings during 1923, showing that the conditions are not unfavourable for this species in the absence of competition. At the lower levels it would find even more congenial surroundings, and observations seem to show that here an actual increase in *Juncus* is in progress.

In the lowest portions and especially where the drainage is rather imperfect extensive areas dominated by *Juncus* occur. The most important species are *Juncus effusus* and *J. conglomeratus*, but in certain places *J. acutiflorus* is co-dominant or dominant, and *J. supinus* also occurs, while many marsh plants which are only rarely found in the *Molinia* consocieties are common here. Throughout the winter the *Juncus* areas form an almost impassable

swamp, the standing water being often over a foot (30 cm.) deep, but in summer a great deal of this swampy region becomes quite dry. On the whole the *Juncus* associates is not so readily colonised by birches as the *Molinia* associates, probably owing to the unfavourable nidus for germination offered by the thick tussocks of crowded upright stems and leaves. Thus the *Juncus* regions at the present time (1925) are generally more open and free from scrub.

The following plants occur in the *Juncus* associates:

<i>Agrostis alba</i>	o.—l.a.	<i>J. supinus</i>	o.—f.
<i>Anthoxanthum odoratum</i>	r.	<i>Lotus uliginosus</i>	o.
<i>Calluna vulgaris</i>	v.r.	<i>Luzula congesta</i>	o.
<i>Carex stellulata</i>	l.	<i>L. multiflora</i>	o.
<i>Deschampsia caespitosa</i>	r.	<i>Molinia caerulea</i>	o.—f.
<i>Erica tetralix</i>	r.—o.	<i>Ranunculus flammula</i>	o.
<i>Holcus lanatus</i>	o.—l.a.	<i>Scutellaria minor</i>	o.
<i>Hydrocotyle vulgaris</i>	o.	<i>Betula alba</i>	r.—o.
<i>Juncus acutiflorus</i>	r.—l.d.	<i>B. pubescens</i>	r.—l.f.
<i>J. conglomeratus</i>	a.—c.d.	<i>Salix cinerea</i>	o.
<i>J. effusus</i>	a.—c.d.	<i>Polytrichum commune</i>	f.—l.a.

(d) *SPHAGNUM* BOGS.

As mentioned above, there are several places on the felled area where *Sphagnum* occurs in quantity, in places becoming sub-dominant. Associated with the bog moss may be either *Molinia* or *Juncus* spp. or more often a mixture of these. From information received it appears that the *Sphagnum* bogs are those which existed prior to felling, so one may perhaps consider that *Juncus* has outstripped *Sphagnum* in the invasion of new areas. The above remarks receive support from the fact that the only stations on the heath for *Narthecium ossifragum* are in the *Sphagnum* bogs. The Bog Asphodel is by no means restricted to such localities on other heaths, so one can only conclude that it has not yet spread into the more recently formed swamps. With *Sphagnum* is also found *Aulacomnium palustre*, sometimes very abundantly.

The full list of plants occurring in the *Sphagnum* bogs is as follows:

<i>Agrostis alba</i>	f.	<i>Juncus supinus</i>	o.
<i>Calluna vulgaris</i>	o.	<i>Lotus uliginosus</i>	r.
<i>Carex stellulata</i>	f.	<i>Luzula congesta</i>	o.
<i>Cirsium palustre</i>	r.	<i>L. multiflora</i>	o.
<i>Erica tetralix</i>	o.—f.	<i>Molinia caerulea</i>	a.—c.d.
<i>Holcus lanatus</i>	o.	<i>Narthecium ossifragum</i>	l.
<i>Hydrocotyle vulgaris</i>	f.—a.	<i>Potentilla erecta</i>	o.—f.
<i>Juncus acutiflorus</i>	f.—a.	<i>Scutellaria minor</i>	o.
<i>J. conglomeratus</i>	o.	<i>Typha latifolia?</i>	r.
<i>J. effusus</i>	f.—c.d.	<i>Viola palustris</i>	o.

Mosses.

<i>Aulacomnium palustre</i>	f.—a.	<i>Leucobryum glaucum</i>	o.
<i>Campylopus flexuosus</i>	f.	<i>Polytrichum commune</i>	f.—a.
var. <i>uliginosus</i>	r.	<i>P. juniperinum</i> (on mounds)	o.
<i>Hypnum fluitans</i>		<i>Webera nutans</i>	
var. <i>falcatum</i>	o.	var. <i>longiseta</i> (c.fr.)	f.
<i>H. stramineum</i>	l.a.		

Mosses (continued).

<i>Sphagnum aquatile</i> var. <i>remotum</i> (floating)	r.	<i>S. cymbifolium</i> var. <i>glaucescens</i>	l.a.
<i>S. auriculatum</i> var. <i>canovirescens</i> (c.fr.)	a.—l.s.d.	<i>S. inundatum</i>	r.
<i>S. compactum</i> var. <i>squarrosum</i>	r.	<i>S. molluscum</i> var. <i>vulgatum</i> (c.fr.)	l.a.
var. <i>semisquarrosum</i>	l.f.	<i>S. plumulosum</i> var. <i>remotum</i> (floating)	o.
<i>S. cuspidatum</i> var. <i>plumosum</i> (floating)	r.	<i>S. obesum</i> (usually floating)	l.a.
		<i>S. recurvum</i> var. <i>majus</i>	l.s.d.

Hepatics.

<i>Gymnocolea inflata</i>	a.	<i>Calypogeia fissa</i>	a.
f. <i>laxa</i>	r.	<i>C. trichomanis</i>	r.
<i>Cephalozia bicuspidata</i>	a.—l.s.d.	<i>Lepidozia setacea</i> (c.fr.)	l.f.
<i>C. connivens</i>	o.	<i>Lophozia ventricosa</i>	r.

Lepidozia occurs in some of the bogs as fine threads binding *Sphagnum* stems closely together, and also sometimes in compact tufts on the ground. Two rather striking absentees are *Leptoscyphus anomalus* and *Odontoschisma sphagni* which are usually characteristic of such bogs.

Zonation of the bryophytes can be detected in the *Sphagnum* bogs, the *Sphagna* themselves showing it most distinctly. The following zones were distinguished by Mr Richards, Zone I being the highest and Zone IV the lowest.

- I. *Sphagnum molluscum* var. *robustum*
S. compactum var. *squarrosum*
var. *semisquarrosum*.
- II. *S. cymbifolium* var. *glaucescens*
S. compactum var. *subsquarrosum*
S. molluscum var. *vulgatum*
S. recurvum var. *majus*
S. auriculatum var. *canovirescens*.
- III. *S. plumulosum* var. *remotum*
S. recurvum var. *majus*
S. auriculatum var. *canovirescens*
S. inundatum
- IV. *S. obesum*
S. aquatile var. *remotum*
S. crassicaudum var. *intermedium*
S. plumulosum var. *remotum*.

(e) DRAINS.

Crossing the felled area there are a large number of drains which vary in size and water supply. Some have permanent streams of running water, others stagnant water in winter only, while yet others are moist in winter only and quite dry in summer. These drains are either shaded to various degrees by young birches or tall *Molinia* or are quite open. Their banks are always more or less sandy, but the floor of many is clayey.

As the conditions in different ditches and in different parts of the same ditch are so varied, the flora also varies greatly in abundance and richness, but in most cases there is a thick carpet of mosses and hepatics on the banks; in this are imbedded small phanerogamic plants. Lichens are almost entirely wanting. On the bottoms of the ditches species of *Juncus* are often abundant.

Of these the most characteristic is *Juncus supinus* f. *fluitans* which is either completely submerged or floats; with this is a floating form of *Agrostis alba*. The only true water plant is *Potamogeton polygonifolius*, this being, however, restricted to the larger drains.

The following examples from Mr Richards give an idea of the variation in the lower plants (Table I):

Drain 1. On edge of wet birch-scrub. Banks very damp, sandy and deep with permanent stream. Shaded.

Drain 2. In *Molinia* consocieties north of North Ridge. Moist in summer, a little stagnant water in winter. Banks of peaty sand. Unshaded.

Drain 3. In drier *Molinia* consocieties. Dry in summer, moist in winter. Banks sandy, mostly shaded.

Drain 4. In upper part of *Molinia* consocieties, near middle of Common. Banks very dry, shaded by thick bramble bushes.

Table I.

<i>On banks</i>		1	2	3	4
Mosses:	<i>Sphagnum cymbifolium</i> var. <i>glaucescens</i>	r.	—	—	—
	<i>S. compactum</i> var. <i>subsquarrosum</i>	—	o.	—	—
	<i>S. recurvum</i> var. <i>majus</i>	r.	—	—	—
	<i>Polytrichum commune</i>	—	—	—	o.
	<i>Ceratodon purpureus</i>	—	—	o. (c.fr.)	—
	<i>Dicranella heteromalla</i>	a. (c.fr.)	—	v.a. (c.fr.)	o.
	<i>Mnium hornum</i>	—	o.	—	—
Hepatics:	<i>Pellia epiphylla</i>	o.	—	—	—
	<i>Cephalozia bicuspidata</i>	a.	v.a.	a.	—
	<i>Calypogeia fissa</i>	la.	f.	f.	f.
	<i>Lepidozia setacea</i>	—	f.	—	—
	<i>Diplophyllum albicans</i>	—	—	—	f.
Lichens:	<i>Cladonia pyxidata</i>	—	—	o.	—
<i>On floor</i>					
	<i>Sphagnum obesum</i>	o.	—	—	—
	<i>S. crassiciadum</i> var. <i>intermedium</i>	—	—	—	o.

In addition to the above the following have been found in ditches at Oxshott: *Calypogeia neesiana*, *C. trichomanis*, *Cephalozia lammersiana* (c. per.), *C. connivens*, *Lophozia excisa*, *Lophocolea cuspidata* and *Dicranella cerviculata* (teste Mr W. R. Sherrin). *Pellia epiphylla*, *Cephalozia bicuspidata* and *Dicranella heteromalla* are the most characteristic species.

These drains are very rapidly colonised by plants, as was shown in the case of one re-cut and widened early in 1922 on the south edge of the damp region. On April 29th there were already a few plants of *Pellia*. The ditch was again examined in February 1923, the following plants being found.

At the top of the sides were *Dicranella heteromalla* and *Polytrichum commune*.

On the sides further down:

<i>Calypogeia fissa</i>	a few stems	<i>Dicranella heteromalla</i>	o.
<i>Juncus supinus</i>	f.	<i>Pellia epiphylla</i>	o.
<i>Pinus silvestris</i>	1 seedling	A <i>Sphagnum</i> belonging to	
<i>Potentilla erecta</i>	1 plant	the <i>subsecundum</i> group	a few tufts

On the bottom in running water was *Juncus supinus* f. *fluitans* (f-a).

The bulbils of the latter—it is usually pseudo-viviparous—are swept along by drainage water; this may explain the rapid colonisation of the ditch. Of the hepatics *Pellia* and *Cephalozia* fruit freely, this being an important factor in producing their wide distribution. In the drier drains *Pellia* is uncommon; here *Dicranella* and *Cephalozia* are co-dominant.

A further examination in March 1924 showed that colonisation had been still more rapid since the previous year. The banks in many places bore large patches of mosses and hepatics, *Dicranella heteromalla*, *Calypogeia trichomanis* and *Cephalozia bicuspidata* being the chief species in the upper portions, while *Pellia* often occurred in a line just above average water level. In one section of the ditch *Diplophyllum albicans* was quite dominant. In the ditch itself were many plants of *Juncus supinus* f. *fluitans* and also scattered individuals of *J. effusus*, the former also growing up the sides in places. *Erica tetralix* was the commonest of the other phanerogams, seedlings and young plants being present all along the sides, mainly near the top. Other plants found were as follows:

<i>Blechnum spicant</i>	1 plant	<i>Polytrichum commune</i>	spreading from top
<i>Calluna vulgaris</i> (seedlings)	o.	<i>Hypnum cupressiforme</i>	
<i>Pinus sylvestris</i> (near top)	r.	var. <i>crucetorum</i>	a few stems
<i>Potentilla erecta</i>	o.	<i>Aulacomnium palustre</i>	1 tuft
<i>Rubus</i> sp. (trailing)		<i>Funaria hygrometrica</i>	1 tuft on a twig
<i>Sphagnum cymbifolium</i> group	o.		

In 1925, although no detailed survey was made it was noticed that the sides were completely covered with mosses and hepatics while large tufts of *Juncus* half choked the bottom of the ditch. Other plants not noticed before were *Betula* (seedlings), *Molinia* (not common but spreading from top) and *Agrostis vulgaris*. It can be seen that the higher plants are the species occurring in the surrounding *Molinia* consocieties and birch scrub. In this part of the ditch phanerogams were not so common as in the more open parts.

(f) BLACK POND.

This can scarcely be termed a part of the felled area, but it seems advisable to describe it here for three reasons: (1) it has been influenced by the felling of the pinewood around; (2) it forms the lowest member in the series of communities from dry to wet conditions; (3) it acts as a centre for the survival of aquatic forms, which can invade any temporary pools formed in the felled area in the vicinity.

Black Pond (see map, 11, p. 289) is a large pool at the western end of the valley in the felled area. A fringe of trees was left around the pond until 1921 when those on the southern side were felled, those on the north and west being untouched. The eastern end tapers to the inlet where it connects with the main drainage of the valley. On the western side is an embankment designed to hold back the water and although it has been broken in several

places the level of the water inside is still higher than the low ground outside. Much of the pond has dried up as a result of these breaks and is now occupied by a marsh which is inundated in wet weather only.

At the inflow end there is a large area of marshy ground dominated by *Juncus effusus* with *J. acutiflorus* forming an almost pure community in the northern part. This is probably the focus from which the *Juncus* invasion mentioned above is taking place. The main N. and S. path crosses the inflow by a bridge which tends to hold up the water. By the inflow stream west of this bridge *Juncus effusus* is again dominant: on either side of it is a zone of *Eleocharis palustris*, *Eriophorum angustifolium* and *Agrostis alba* co-dominant, these grading into the *Molinia* consociates on drier ground; willows (*Salix cinerea* and *S. fragilis*) occur among the rushes. To the north of the pond the ground rises rapidly, so that on this side the zonation is sharp and some of the zones are lacking. At the western end is a large irregularly shaped sheet of open water, but most of the pond is filled with a tall reed-swamp of *Phragmites vulgaris* which grows either in the water itself or on ground which is dry during the summer. On the north *Phragmites* comes right up to the bank: on the south it was burnt away by the 1921 fires and replaced temporarily by *Eriophorum angustifolium*. In 1925 the *Phragmites* had partially recovered in this region, there being scattered haulms about 2-3 ft. (60-90 cm.) in height. Here, as well as in the drier parts of the reed swamp, many young trees of *Betula* are growing and the whole will ultimately pass into woodland. A transect across the pond in 1921 gave the following zonation (Fig. 4). *Reed Swamp*. Near the open water in the centre this is almost pure *Phragmites*—*Typha latifolia* occur in one place on the western side—but where the ground is relatively drier there are a number of other plants growing among the stems of the reed. They are:

<i>Betula alba</i>	o.—l.a.	<i>Hypochaeris radicata</i>	r.
<i>B. pubescens</i>	o.—l.a.	<i>Juncus acutiflorus</i>	o.
<i>Eleocharis palustris</i>	o.	<i>J. effusus</i>	o.
<i>Epilobium angustifolium</i>	r.	<i>J. supinus</i>	f.
<i>Eriophorum angustifolium</i>	f.—a.	<i>Molinia caerulea</i>	o.
<i>Hydrocotyle vulgaris</i>	f.	<i>Viola palustris</i>	r.
<i>Hypericum elodes</i>	r.		

Some of these are obviously invaders from the dry areas around. In the water itself where it comes to the bank is *Scirpus fluitans*.

The following *Sphagna* grow in the reed swamp, usually in the wetter parts, especially where the ground rarely dries out.

<i>Sphagnum plumulosum</i> var. <i>remotum</i>	l.a.	(in water up to c. 10 cm. deep)
<i>S. cuspidatum</i> var. <i>plumulosum</i>	l.a.	(water from c. 5-30 cm. deep)
<i>S. obesum</i>	a.	(water from c. 25-30 cm. deep)
<i>S. franconiae</i> (probably only a form of <i>S. obesum</i>)	a.	(water from c. 25-100 cm. deep)

The last named grows abundantly in the reed swamp and as large floating masses in the open water beyond, as well as more sparingly in some of the neighbouring ditches. *S. recurvum* forms large beds almost

entirely at the eastern end of the pond. *S. cuspidatum* var. *plumosum* grows characteristically in small scattered groups in shallow water, especially in small pools separated from the main pond in summer. None of the *Sphagna* of the upper zone of the damp series occurs around Black Pond.

The following Bryophytes occur in the area with much *Eriophorum* on the south side of the pond or elsewhere.

Aulacomnium palustre	f.	<i>Sphagnum serratum</i> (Mr W. R. Sherrin)	
Cephalozia bicuspidata	f.	<i>S. amblyphyllum</i>	o.
Hypnum fluitans var. falcatum	f.	<i>S. recurvum</i> var. <i>majus</i>	l.a.
<i>Sphagnum papillosum</i> var. <i>normale</i> (comm. Mr W. R. Sherrin)			

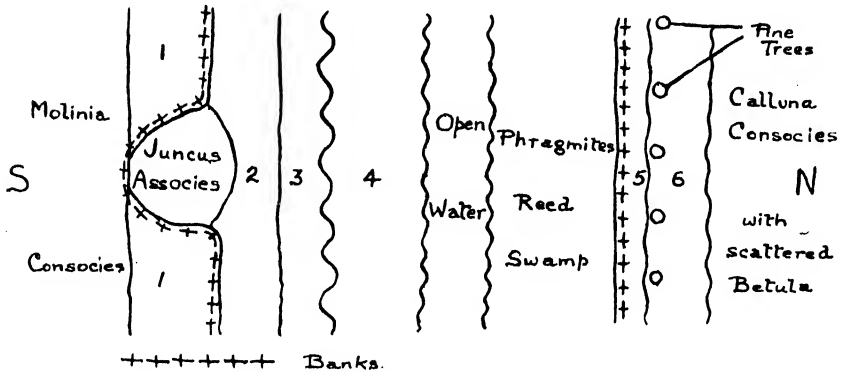


FIG. 4. Diagram of belt transect across Black Pond from N. to S. to show zonation of communities. 1. *Molinia-Juncus* ecotone. 2. *Eriophorum* and *Agrostis alba*. 3. *Eriophorum* and *Phragmites*. 4. Reed swamp of *Phragmites*. 5. *Agrostis alba*. 6. *Molinia* consocias.

It is obvious from the ordnance maps that this silting up of the pond and invasion by reed swamp, etc., has been in progress for many years. Even in 1912 there was very little open water, but it is probable that the reed swamp was in much deeper water then. In any case the felling of the surrounding wood has accelerated the process by increasing evaporation while the blocking of the drainage in the valley farther up has reduced the amount of water inflowing.

(II) The Birch Phase.

Since we first visited the district in 1920 active colonisation by *Betula* has been taking place so that now there are all gradations between close birch-scrub with undergrowth of *Molinia*, etc., and open *Molinia* with few birches.

Where the *Molinia* consocias is in close contact with plantations containing birches, or near mature birches left after felling, the area is rapidly being converted into birch scrub. On the east of the Common is a large circular felled region, termed by us the "Inner Circle" (see map, 11, p. 289). When we first visited this in 1920 it consisted of typical *Molinia* consocias with a number of small birches about 18 in. (45 cm.) high. At the upper (southern)

margin was a zone of almost bare ground with scattered and even smaller birches. In 1923 the lower part was still predominantly *Molinia*, but the birches there were from 4–5 ft. (1·2–1·5 m.) in height while the upper portion, including the originally bare zone, had been converted into a thick birch scrub nearly 7 ft. (2·1 m.) in height. In the upper portion were also numerous pine seedlings of various sizes. There have been several superficial fires in the region during this period but except in the south-west corner they have had little effect on the colonisation. This region is surrounded by mature birches and pines on most sides and this explains the rapid invasion. In 1925 the conditions were much the same but the scrub in the southern half was very tall and thick while there were quite tall pines (up to 6 ft. = 1·8 m.) among the birches.

In other regions the birch scrub was even better developed, but unfortunately most of it was destroyed by fire in 1921. Nevertheless the birch has made a wonderful recovery in these regions and the scrub is almost as thick as previously. As will be seen from the map, the most prominent belt of scrub occurs around the periphery of the felled area and then gradually thins out towards the centre.

In certain damper parts of the pinewood prior to felling there were a number of small *Castanea*, Birch and other trees under the pines. When the latter were felled the *Castanea*, etc., grew well, forming a scattered scrub in these parts of the developing *Molinia* consociates. It is probable that this *Castanea* zone, which occurs typically on the southern edge of the felled areas (see map) represents the distance to which *Castanea* had invaded the pinewood from the great plantation adjacent. It was shown previously (11, p. 298) that *Castanea* is able to establish itself under *Pinus*—germinating seeds and young plants have been found—and it is almost certain that it was not planted here since the pinewood was subspontaneous, although in the woods around planting was carried out. Many of the chestnut trees were badly damaged or killed during the fires so that this zone is not now so prominent, but the taller isolated trees still stand out amidst the more recent thick birch scrub.

As the trees grow up the ground vegetation becomes gradually suppressed, so much so that the ground is often almost bare under the young trees. *Calluna* is usually the first victim, while *Molinia*, *Juncus* and *Erica tetralix* persist longer, but even they become etiolated and do not flower. *Betula* casts a deeper shade than is usually ascribed to it in books, particularly in the young stages when the lower branches grow horizontally only a few inches above the ground. Later on, as the trees grow up, their growth becomes more open and a certain amount of recolonisation takes place, but in thick birch scrub *Calluna* and *Erica tetralix* never regain their lost positions.

In the damp regions *Betula pubescens* becomes co-dominant with *B. alba* or even outnumbers it, especially in the wetter places. Very few new plants

seem to be associated with the development of the birch scrub. Young trees of *Castanea*, *Quercus robur*, *Q. cerris*, *Sorbus aucuparia*, *Fagus sylvatica*, *Prunus avium* and *Pinus silvestris* are dotted about, but in general the ground vegetation is simply an impoverished and stunted *Molinia* or *Juncus* associates.

In a few places the felling was not complete, sometimes owing to the relatively high proportion of deciduous trees originally present. In these regions conditions are rather different from those in the completely felled areas as seeds of these species are available in large quantities. A number of mature trees of *Betula*, *Quercus*, *Castanea*, *Fagus*, etc., were left scattered about and within this region a scrub has rapidly formed. Young trees of *Quercus* and *Betula* predominate, but other species occur. The ground vegetation is a mixture of *Pteridium*, *Molinia* and *Rubus* growing together in inextricable confusion and obviously in active competition—probably all survivors from the original wood. This scrub will in time be converted into Mixed Wood of the usual type, and possibly illustrates a further stage in the march of colonisation, the younger stages of which occur on other parts of the felled region. Few pines have yet appeared here.

(III) *The Pine Phase.*

Indications of a future development of this are much more evident on the wet areas than on the dry ones. Young pines occur abundantly among the *Molinia* and in the birch scrub, especially in regions abutting on the unfelled pinewood or on plantations containing pines, and there seems no doubt that another pine colonisation is in the first stages of development. At present, with the exception of several small clumps of pines from openings in the original wood and not felled with the other trees, none of the trees is over 10 ft. (3 m.) in height, and few exceed 5 ft. 6 in. (1.65 m.), representing trees eight years of age which appeared the year after the felling. Other trees of all sizes from 3 in. (7.5 cm.) upwards occur, and are in most cases thriving except where they are slightly etiolated owing to shading by the birches, or in the very wettest places. *Pinus* apparently does not succeed in soil in which the saturation point is maintained for any length of time, such conditions resulting, in the case of the larger plants, in an extraordinarily slow rate of growth, and in the seedlings dying at about two or three years of age.

Unfortunately *Pinus*, owing to its resinous tissues, suffered more severely than almost any other plant in the fires, otherwise it would be much commoner than it is. Since the crop which germinated from seed left after felling was mainly killed by fire, it is now left to wind to carry seeds into the interior of the felled area, and apparently wind, in spite of R. Smith's observations (10), is not a particularly effective agent of dispersal in the case of *Pinus*. At any rate the number of seeds carried more than 100 to 150 yds. (90–135 m.) from mature trees is not sufficient in view of the activity of agents destroying

the seeds and seedlings after dispersal. In the course of some sowings *in situ* carried on in 1925 something of the effect of these destructive agents was seen. A detailed map of the pine seedlings on part of the damp areas was made early in 1925, and it was surprising how few young plants (under 5 years) there were outside a radius of 130 yds. (117 m.) from the edge of the unfelled wood or from other mature trees. There seems no doubt however that, given a reasonable freedom from fires, especially during the next few years—larger trees are not so susceptible as younger ones—*Pinus* will gradually recolonise the wet areas and reconvert them to pinewood.

(IV) General Remarks.

The succession on the damp areas may be expressed in the following scheme (Fig. 5).

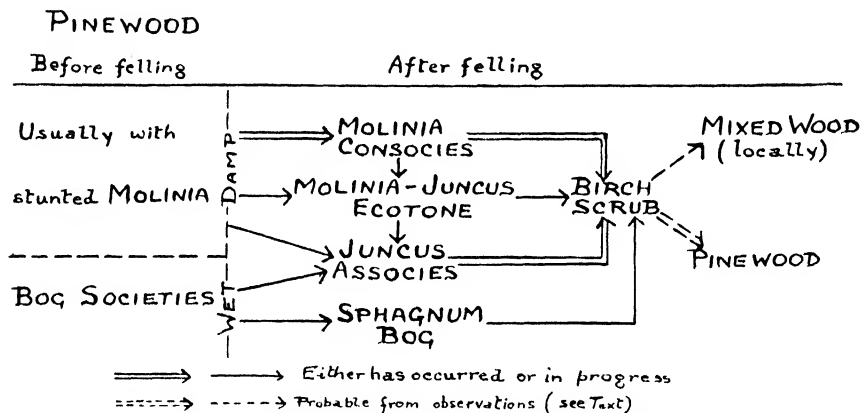


FIG. 5. Scheme of colonisation of the damp regions.

In all probability the *Juncus* and *Sphagnum* communities will not become colonised very quickly unless the drainage is improved. *Betula* can tolerate very great extremes of water content in the seedling stage, but the conditions among *Juncus* and *Sphagnum* with a thick layer of rotting saturated litter on the ground are not favourable for germination. This was well seen in an area adjacent to a well-developed birch wood on the east side of the Common. Although seedlings by the hundred occurred among *Molinia* and mixed *Molinia* and *Juncus*, yet in an almost pure zone of *Juncus effusus* nearer the wood hardly a seedling was to be seen. As mentioned above, *Pinus* is practically never successful in such localities.

C. TRANSITIONAL REGIONS.

In several places the sharp line between the wet and dry series communities is not present. This is due to the gradual slope from the higher to the lower ground resulting in a wide transitional zone, in which the dominants of the two adjacent types are in active competition. It has already been mentioned

of killed and damaged *Molinia* alternated frequently, the burning often being worst around the pine stumps. The *Castanea* trees were very badly damaged, many of them failing to sprout until 1923, while some quite large trees were completely killed. The birches were severely injured, being exterminated in many places and extensive tracts of birch scrub were entirely consumed. A thick layer of charred materials was left everywhere. The very wet *Juncus* communities suffered less, but even they were sometimes killed, while the *Phragmites* in Black Pond was half burnt over. As others have noted (6, p. 118), the courses of fires are very capricious, and no doubt some areas were burnt several times while others were either missed altogether or were burnt very slightly.

A. DRY REGIONS.

In dry regions the recovery, except in one particular, has been very slow.

1922. In April numerous seedlings of *Epilobium angustifolium* were seen in depressions on the ridge; these grew up and flowered in the same year. In some places the birches sprouted, but generally they were entirely killed. *Pteridium* sent up a few scattered fronds of small size in many places, and was perhaps on the whole less affected than any other plant. Some of it however was completely killed and has shown no sign of life since. Digging in this area revealed dead, decaying rhizomes—probably killed by the heat. In addition to removing the peat layer the fire had so hardened the sand beneath that locally it was almost like rock, this being very inhospitable ground for germinating seeds. On terrain of this type *Hornidium flaccidum* was found in a thin macroscopic green layer.

1923. Little change had taken place in some of the burnt regions but in others the birches had sprouted quite successfully and seemed to have recovered completely, while *Pteridium* was growing much as before the fire. *Epilobium* had spread very considerably, covering large areas. On the northern slope of the ridge *Funaria* was growing well in extensive patches, but had not fruited: it is interesting to note that the same stage was reached on the damp areas in 1922. *Bryum argenteum* was also seen in a few places and fruited in October. *Hieracium pilosella* and *Rumex acetosella* were noticed here and there, but the latter was not so common in the dry regions here as on other heaths. Seedlings of *Senecio silvaticus* appeared late in the year.

In one place at the base of the dry area all the burnt plants of *Ulex nanus* had sprouted from the stools, while the other members of the original *Calluna* consocieties here had been killed. *Ulex* was therefore dominant, which it otherwise never is (5). The exposed bushes were nibbled into cushions by rabbits, while the plants in the shelter of small birches were large and flowered profusely.

1924. This year *Ceratodon purpureus* appeared in quantity for the first time on the dry areas, replacing *Funaria* in many parts; in others, however, *Funaria* was still the dominant moss. *Epilobium angustifolium* also continued



FIG. 1. Dry area. Birch as the prime coloniser on burnt ground. *Epilobium angustifolium* can be seen in the middle distance. Soil between plants perfectly bare. Oct. 1925 (see p. 235).

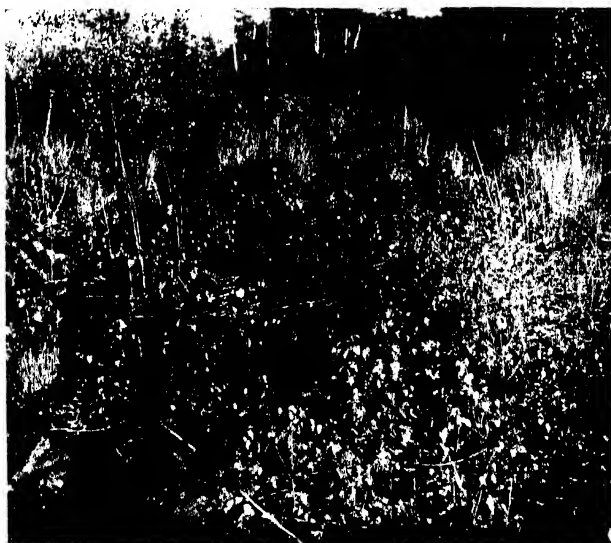


FIG. 2. Damp area. Burnt patch in *Molinia* consociates with carpet of *Polytrichum* and many young bushes. Oct. 1925 (see p. 239).

its spread and formed in some parts thickets some 3 or 4 ft. (90–120 cm.) in height. Later on in the year many seedlings of *Calluna* and *Betula* grew up under the shade of the willow herb. Birch and heather seedlings also appeared in the barer burnt patches, while locally *Senecio silvaticus* was abundant, flowering profusely. Other plants found included *Sonchus oleraceus* and *Taraxacum officinale* (both common weeds of non-acid soils around), their growth being no doubt favoured by the less acid soil reaction.

In several places, however, the development was not so far advanced. On the north slope of the ridge there were in November extensive carpets of *Ceratodon purpureus* mixed with *Polytrichum formosum*, in which birch seedlings were decidedly rare, while *Epilobium* was present only as scattered clumps. The advent of the *Polytrichum* marked a further stage in the reversion to the original acid substratum.

On the regions in which the surface had been burnt quite hard an interesting extra phase had been interpolated, and here was seen almost the only example on the Common of a cryptogamic phase being necessary before the higher plants could colonise the ground. Darker patches of this hard surface were found on investigation to be damper than the normal owing to the presence of a thin film of mucilaginous soil algae. On these patches there appeared afterwards *Ceratodon* and *Polytrichum*, but in 1924 very few higher plants arrived. The mosses were not seen on the ordinary baked surface.

1925. No marked change had taken place up to September of this year. *Epilobium* was maintaining itself on most of the areas, although it had certainly decreased in luxuriance. *Polytrichum* had replaced *Ceratodon* in many places, and many young plants of *Betula* (Plate III, fig. 1) and *Calluna* had established themselves. *Pteridium* commenced to recolonise the burnt areas around the remnants left by the fire.

General Remarks. It may be seen that on the drier burnt regions the re-establishment of the original vegetation has commenced, but has not yet progressed far, while temporary communities still hold the field in most places.

B. WET REGIONS.

1921. Where the *Molinia* was only moderately burnt it recovered quickly, a short thick turf being produced by the autumn after the fire, but no flowers. Seedlings of *Epilobium* and *Senecio silvaticus* appeared on the quite bare patches.

1922. The *Molinia* sprouted, producing inflorescences about a foot (30 cm.) high. *Betula* and *Quercus* also sprouted everywhere while a few plants of *Castanea* showed signs of life.

Meanwhile on the perfectly bare areas a rapid colonisation set in. Many seedlings of *Epilobium* appeared and those both of this species and of *Senecio* from the previous year flowered. This rapid appearance and spread of *Epilobium* and *Senecio* was no doubt due to the increased nitrification in the soil

following burning (see pp. 210 and 213). At the same time the ground became green with moss protonema, mainly of *Funaria hygrometrica* which developed and in a few places fruited; by July some of the previously bare patches were completely covered with this moss. Kessler (9, p. 369) has shown that the spores of *Funaria* will only germinate in an alkaline medium; this is provided for them by the salts in the ash left after the burning of the humus and litter. *Ceratodon purpureus* was also present but in very small amount. Annual plants such as *Rumex acetosella* appeared in great numbers, while many plants of *Deschampsia flexuosa* had arrived in parts of the burnt Molinietum.

In July in the drier parts of the *Molinia* consociates numerous seedlings of *Calluna* appeared, while in one or two districts a large number of seedlings of *Digitalis purpurea* sprang up. The origin of these is a mystery, as there were none flowering on the heath, but they probably came from a garden since in 1923 some had white flowers: the nearest garden was however a long way off. Other phanerogams which were observed on the burnt patches in 1922 were *Cerastium vulgatum*, *Epilobium montanum*, *E. roseum*, *E. tetragonum*, *Erigeron canadense*, *Hieracium pilosella*, *Holcus lanatus*, *Hypochaeris radicata*, *Rumex acetosella*, *Sagina subulata*, *Senecio silvaticus*, *S. vulgaris*, *Sonchus oleraceus*, *Stellaria media*, *Taraxacum officinale*, *Trifolium dubium* and *T. repens*, most of which are common weeds with excellent means of seed dispersal.

At the edges of the completely burnt patches there was a slight slope, and here a number of sporelings of *Pteridium* appeared. Apparently the conditions of moisture, etc., due to the hygroscopic nature of the layer of charred organic material present were suitable for the production of prothalli. *Polytrichum commune* and *P. juniperinum* arrived after *Funaria* especially in the wetter parts of the burnt patches, while *Marchantia* appeared locally in large quantities.

Taken as a whole, it may be said that apart from *Epilobium* the main development was by lower plants, mosses being most prominent. Owing to the greater moisture these get established much more quickly than on the usual dry type of heath. The first of the series of quadrat charts (Fig. 6) gives an idea of the condition of a typical completely burnt area in 1922, the scattered *Epilobium* plants being about 2 ft. (60 cm.) high.

1923. The mosses spread more, a great deal of the original burnt out ground in February being converted into green carpets of *Funaria* and *Polytrichum*, the former fruiting everywhere; *Bryum argenteum* was only common locally. *Polytrichum piliferum* appeared and *Ceratodon purpureus* fruited in many places. Later on in the year this moss became much more prominent and had apparently replaced *Funaria* in many places. This phase usually occurs after burning, when most, but not all, of the salts from the wood-ash have been washed out of the soil. *C. purpureus* is a moss noted for its extraordinary range of habitat and indifference to soil constitution; for instance, it grows well on both chalky soil and peat, though perhaps it has a preference

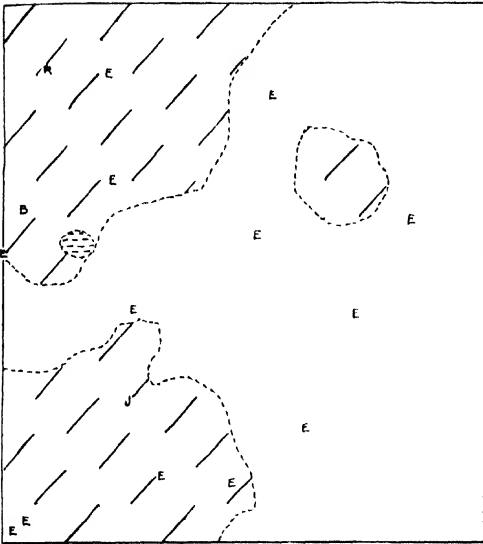


FIG. 6. 1922.

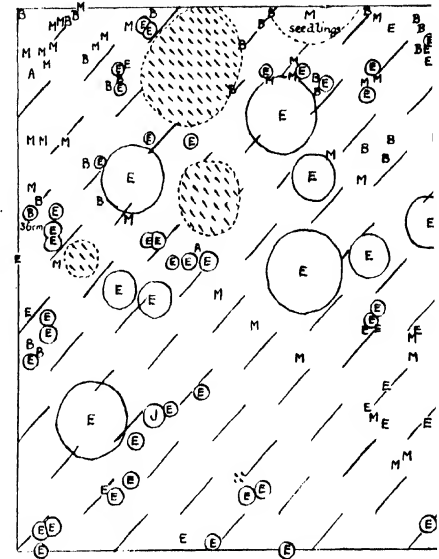


FIG. 7. 1923.

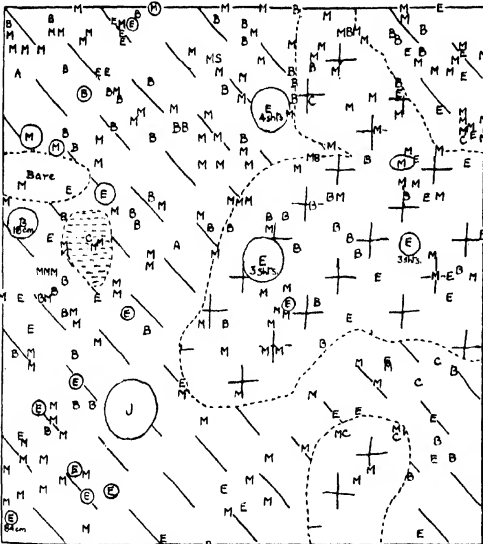


FIG. 8. 1924.

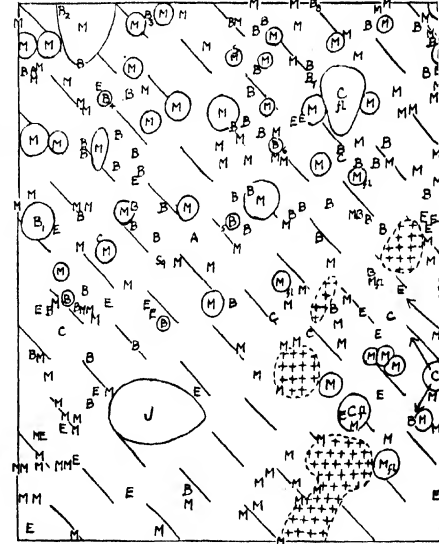


FIG. 9. 1925.

These are charts of the same quadrat made in the years 1922-25. The quadrat is 1 square metre in area. The symbols, etc. are used in all the charts. Single letters represent seedlings or small shoots; the circles or other indicate the areas of the larger plants, the number of shoots being given in some cases; the heights of certain plants given.

A., *Sorbus aucuparia*. B., *Betula* spp. C., *Calluna vulgaris*. E., *Epilobium angustifolium*. J., *Juncus conglomeratus*. M., *Molinia caerulea*. R., *Epilobium roscum*. S., *Salix cinerea*. Sq., *Juncus squarrosus*. = = = = *Marchantia polymorpha*. / / / *Funaria hygrometrica*. + + + + *Ceratodon purpureus*. \ \ \ \ \ *Polytrichum* spp. (mostly *P. juniperinum* and *P. formicetorum*).

FIG. 6. The *Epilobium* here was about 60 cm. high.

FIG. 7. A thick growth of *Epilobium* approx. 1 m. high filled the quadrat although the stems seem scattered in the

FIG. 8. *Epilobium* almost as tall but much thinner.

FIG. 9. Tallest *Epilobium* shoot inside quadrat = 58 cm. B₁ 7 shoots, highest 34 cm., B₂ 30 cm., B₃ 23 cm., B₄ 24 cm., B₅ 16 cm., B₆ 22 cm., B₇ 3 shoots, 10 cm., B₈ 21 cm., B₉ 2 shoots, 16 cm. Arrows indicate prostrate branches. fl = flower.

for neutral and acid soils. As it is such an abundant species and fruits so readily, its spores must always be present in the atmosphere in a district like Surrey, and as the soil becomes less suitable for *Funaria* it becomes more so for *Ceratodon*. *Marchantia* also continued its spread. In the burnt areas in both years many fruit bodies of *Laccaria laccata* were seen, together with other rarer species.

The most striking development however was that of the phanerogams. On the partially burnt areas *Molinia* grew to its normal size and, in the damper areas particularly, produced inflorescences up to 3 ft. 6 in. (1 m.) in height. *Betula* also grew very well and seemed to have recovered completely, while a large number of *Castanea* trees which had shown no life in 1922 sprouted at the bases of the trunks.

On the burnt patches *Epilobium* was easily dominant, filling the drier places with a close vegetation 3-4 ft. (c. 1 m.) high, while later in the year the air was a mass of flying seeds which became entangled in everything. Many seedlings of *Betula* on the drier parts, and of *Molinia* and *Juncus effusus* on the damper, grew up during the year, while in some of the wetter regions *Holcus lanatus* was extremely abundant. Seedlings of many other plants also appeared, such as *Erica tetralix*, *Calluna*, *Deschampsia flexuosa*, *Juncus squarrosus* and *J. supinus*, these being members of the regular heath flora. The annuals and biennials, including various weeds, *Senecio silvaticus*, *Rumex acetosella* and *Digitalis* also increased in amount. *Aira praecox* and *Senecio jacobaea* were fresh arrivals in 1923.

Fig. 7 shows the same quadrat one year later (1923). The dominance of *Epilobium* is apparent, the willow-herb in this patch forming a thick stand over 3 ft. (c. 1 m.) high. The arrival of seedlings of *Betula*, *Molinia* and *Calluna* is evident.

1924. In this year the inauguration of two fresh phases in the succession could be seen. In the first place *Epilobium angustifolium*, which was quite dominant in many burnt patches in 1923, began to lose ground. Most of the plants were decidedly less luxuriant and showed a xerophilous structure normally associated with later phases in a burn succession. Other work done by us on *Epilobium* shows that this can be definitely related to the decrease in available nitrates.

In addition a great number of seedlings of *Molinia* and *Betula* could be found everywhere growing beneath the *Epilobium* and forming the vanguard of the next phases. At the same time *Polytrichum* spp., mainly *P. commune* and *P. juniperinum*, appeared in large quantity, *Ceratodon* being less conspicuous though still plentiful, while *Funaria* was banished to drier knolls where the succession was not so far advanced. Polytricha always become abundant when the last traces of the soluble salts in the ground have disappeared and the soil reverts to its former acid condition.

In the very wet parts *Juncus effusus* and *J. conglomeratus* had entirely

filled the burnt patches with a thick growth of young plants, while several of those which had appeared in 1923 produced small inflorescences. In one area, where the completely burnt region was more continuous than usual, *J. effusus* now formed an almost pure stand where formerly *Molinia* had predominated. The other members of the normal *Molinia* consociates also increased, some of them being very abundant locally.

An interesting feature in 1924 was the appearance on the damper burnt patches, especially those on which *Polytrichum commune* was dominant, of numerous seedlings of *Pinus silvestris*. Some of these no doubt grew up in 1923, but they were first noticeable in the following year, being then from 3 to 9 in. (8-23 cm.) in height. Many however seemed to be rather unhealthy, and probably will not survive, at any rate not in the wettest places.

Fig. 8 shows the state of colonisation of the same quadrat in 1924. The decrease of *Epilobium* and the increase in the other plants is very striking, also the almost complete dominance of *Polytrichum* spp.

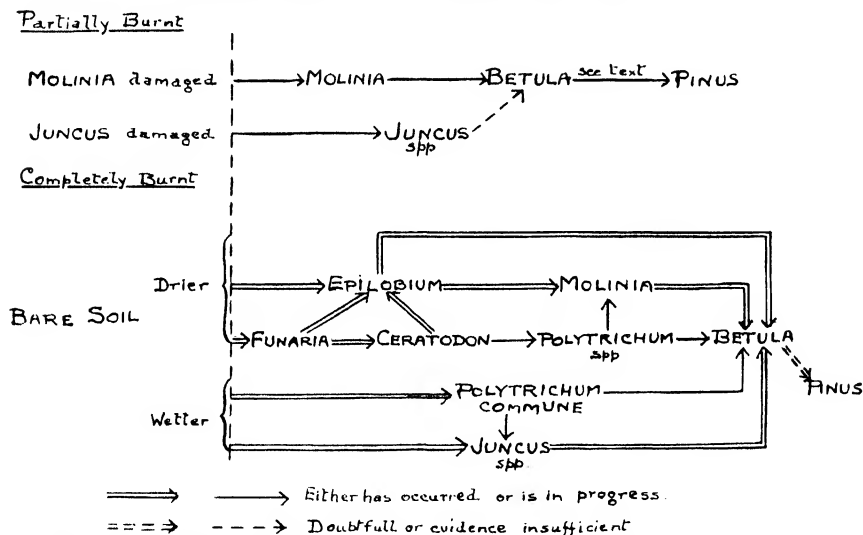


FIG. 10. Scheme of secondary successions following burning on the damp regions.

1925. The changes noted in 1924 were carried farther this year. *Epilobium* had almost entirely disappeared from many burnt patches, while many low thickets of young birches up to 18 in. (45 cm.) in height had grown up, these being very prominent in the less wet regions (Plate III, fig. 2). *Polytrichum* spp. (*P. formosum* and *P. juniperinum*) were almost entirely dominant in these places. On the wetter parts *P. commune* was the chief moss, usually associated with *Juncus* spp. Birches were abundant here also, although perhaps not in such large numbers as on the drier patches. *Molinia* had also increased greatly while *Calluna* was common locally. The fourth quadrat chart (Fig. 9) shows the state of a typical burnt region in 1925 and illustrates

some of the above points. It can be seen from the foregoing that the species of the typical wet soil community are quickly asserting themselves and that colonisation is extremely rapid. The sequence of colonisation on the damper burnt areas so far as it is known is represented schematically in Fig. 10.

In many places, owing to the rapid growth of birches on the burnt patches, the *Molinia* phase will become telescoped, the other communities passing direct into birch scrub. Where, however, the burns are away from the mature birches the *Molinia* consociation is re-establishing itself quite successfully. The initiation of the pine phase is also evident, though it will be some time before the pines will be of any importance on the burnt patches.

3. COMMUNITIES OF SPECIAL HABITATS

Under this heading we class communities which cannot be brought into a general scheme elsewhere.

(a) *Ruderal Communities*. There are places where the direct influence of man has greatly modified the vegetation and often made it possible for species alien to heath conditions to flourish. The track along the north end of the Common has been reinforced with clinker and earth and as a result a number of weeds and other plants are to be found there. Some of these have spread in places into the felled area adjacent and are there competing with the heath flora. In other places similar plants are found by smaller paths. In 1922 the following "weeds" occurred:

<i>Arctium lappa</i>		<i>Ranunculus repens</i>	
<i>Cirsium arvense</i>	f.	<i>Rumex crispus</i>	f.
<i>C. lanceolatum</i>	f.	<i>Sonchus oleraceus</i>	
<i>Hordeum murinum</i>		<i>Stellaria media</i>	
<i>Lotus corniculatus</i>		<i>Taraxacum officinale</i>	
<i>Potentilla reptans</i>		<i>Trifolium repens</i>	
<i>Plantago lanceolata</i>		<i>Tussilago farfara</i>	
<i>P. major</i>		<i>Urtica dioica</i>	
<i>Polygonum aviculare</i>		<i>Veronica serpyllifolia</i>	
<i>P. hydropiper</i>	f.	<i>Vicia sativa</i>	
<i>Prunella vulgaris</i>			

Polygonum hydropiper is typically found by paths in many places; its presence is probably correlated with the increased water-content due to trampling of the ground; the seeds may also perhaps be distributed in the mud on boots. Some of the above species, e.g. *Cirsium arvense* and *Rumex crispus*, are always found in waste places on the heath. There are also several rubbish heaps on the felled areas, especially a large one in the Great Hollow. On these were found various weeds and other plants. The following which have appeared in the Great Hollow at various times give an idea of the flora of these heaps:

<i>Atriplex patula</i>	<i>Polygonum persicaria</i>
<i>Capsella bursa-pastoris</i>	<i>Populus alba</i> (young)
<i>Cerastium vulgatum</i>	<i>Senecio silvaticus</i>
<i>Chenopodium album</i>	<i>Sonchus oleraceus</i>
<i>Corylus avellana</i> (young)	<i>Taraxacum officinale</i>
<i>Digitalis purpurea</i>	<i>Teucrium scorodonia</i>
<i>Erigeron canadense</i>	<i>Veronica arvensis</i>
<i>Mahonia aquifolium</i>	

An interesting addition was *Epilobium angustifolium* which by 1924 had completely overrun the above-mentioned large heap, this again being an example of its preference for spots rich in available nitrogen.

A rather exceptional habitat is the large heap of sawdust (50 yds. = 45 m. long and several feet thick in the middle) in the north-west corner of the heath: other heaps occur elsewhere. This sawdust is apparently a very inhospitable substratum for plants, since even in October 1923 practically nothing but a few small birches could be found on it. At the edges *Molinia* was trying to push through, but looked rather unhealthy. By October 1925 only a few seedlings of *Erica tetralix* had been added. That the sawdust becomes a suitable habitat later on is shown by the fact that a small mound (6 ft. \times 4 ft. and over a foot deep) in another place had *Cirsium arvense*, *Anagallis arvensis*, *Solanum nigrum* and *Cerastium vulgatum* growing on it—a typical weed flora. Hesselman (8, résumé, p. c) states that sawdust on partial decomposition nitrifies actively and that nitratophilous plants then occur on it. The wood of *Pinus*, owing to the large amount of resin present, seems much more resistant to micro-organisms than other woods, and this accounts for the slow rate of decomposition of the Oxshott sawdust. In November 1923 on one sawdust heap the fungus *Tremellodon gelatinosum* was abundant.

(b) *Pine Stumps*. The stumps of the felled trees, which are scattered fairly regularly over the whole area, have a somewhat special flora which is composed mainly of fungi. At first, owing to the resinous nature of the wood and general unsuitability of the surface, the stumps remained bare. Later on the bark especially gradually decayed and many fungi were found growing on it or between the bark and the wood itself. The following have been found:

Corticium albo-stramineum		Polyporus amorphus	
Flammula sapinea	a.	P. hispidus	
Fomes annosus		P. mollis	
Hypholoma fasciculare	a.	P. tephroleuca	
Lenzites saepiaria		Polystictus versicolor	
Merulius tremellosus		Sparassis crispa (mostly on burnt stumps)	
Paxillus involutus		Thelephora lacinata	f.
Pholiota spectabilis	f.	Trametes gibbosa	
Pluteus cervinus (albino form)		Tremellodon gelatinosum	

In addition to these were *Polyporus schweinitzii* with *Hypholoma* and *Thelephora* on the roots. On the cut surfaces, especially associated with the holes of wood-boring beetles, *Calocera viscosa* and *Dacryomyces* sp. were found. The myxomycetes *Lycogala epidendrum*, *Fuligo septica* and *Stemonitis* sp. occurred plentifully both on the wood and on the bark.

Mosses also appeared at a fairly early stage although not frequently. The following have been found, mostly on the bark or on rough parts of the cut surface where a little mineral matter collected:

Aulacomnium androgynum	r.	Eurhynchium praelongum	
*A. palustre	o.	Hypnum cupressiforme	o.
*Brachythecium velutinum	r.	var. resupinatum	r.
Bryum erythrocarpum		*var. tectorum	
Ceratodon purpureus	o.	Tetraphis pellucida	
Dicranum scoparium	o.	Webera nutans	o.

Those marked with an asterisk were sometimes found on the smooth cut surfaces.

A certain number of lichens were also present. *Parmelia physodes* and *Cladonia pyxidata* sometimes occurred on the cut surfaces, but most of the lichens come in when the stumps are more decomposed. Other lichens besides those mentioned above are: *Cladonia silvatica* (r.), *C. furcata* (v.r.), *C. macilenta* (l.), *C. parasitica* (l.), *Lecanora varia* (o.), and *Lecidea uliginosa* (v.r.).

In some cases the stumps have gradually decayed away and merged into the surrounding soil, but in many cases a rather different state of affairs has come about. The inner portion of the stumps has either been burnt out or has decayed away leaving a small depression. In such places soil of a sort has collected and formed a suitable nidus for the establishment of higher plants. In 1924 the following were found in various stumps: *Epilobium angustifolium*, *Fagus silvatica* (seedling), *Ranunculus repens*, *Betula* (seedlings) and *Rubus* spp. In 1925 *Molinia caerulea*, *Sorbus aucuparia* and *Deschampsia flexuosa* were also seen, while *Epilobium* was relatively frequent in hollow or decayed stumps. In the November of 1924 it was noticed that the stumps were rapidly rotting away inside although often preserving a smooth and rigid outer shell. No doubt within a few years they will have almost completely disappeared.

4. SUMMARY AND CONCLUSIONS

1. The recolonisation of an area of felled sub-spontaneous pinewood is described.

2. The progress of colonisation and the communities formed are dealt with, it being shown that different lines of succession are followed on dry and wet areas.

3. On the former ordinary dry-heath communities of *Calluna* and *Pteridium* are being formed, while *Betula alba* and *B. pubescens*, in addition to forming pioneer communities themselves, are invading the other parts. The distribution and advance of *Epilobium angustifolium* are especially fully treated, while data as to powers of dispersal, etc. of other species are given.

4. On the wet regions the main dominant is *Molinia caerulea* which covers large stretches. *Juncus* spp. (especially *J. effusus* and *J. conglomeratus*) seem to be invading these *Molinia* communities. All the consociates on the damper parts are ahead of the drier types in development and are completely closed. Two factors are suggested to explain this: the presence of *Molinia* in the damp parts of the original wood and the more favourable soil conditions in these areas after felling.

5. Young trees of *Betula* spp. are to be found everywhere; it seems as though both wet and dry regions are being converted into a scrub, mainly of birches, and finally into woodland. The small part played by *Pinus* in the primary phases of the process is noteworthy, but the evidence suggests that eventually, on the damp areas at least, pinewood will be re-established.

6. The effect of fires on the felled region is described. In particular the disastrous fires of 1921 are dealt with, and it is shown that burning greatly alters the course of colonisation. The new successions initiated are followed in detail, the wet and dry regions agreeing in that *Funaria* and *Epilobium angustifolium* are the dominant plants in the earlier stages, while later on *Ceratodon* replaces *Funaria*; but after this the successions diverge, the usual dominants of the two regions, viz. *Calluna* on the dry areas and *Molinia* and *Juncus* spp. on the damp areas, becoming more abundant. *Betula* seedlings also appear at an early stage and this will probably result in a telescoping of some of the normal stages.

7. The special floras of ruderal areas and of the pine-stumps are described.

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STUDIES ON THE ECOLOGY OF ENGLISH HEATHS

III. ANIMAL COMMUNITIES OF THE FELLING AND BURN SUCCESSIONS AT OXSHOTT HEATH, SURREY

By O. W. RICHARDS.

(*With twenty-nine Tables and two Figures in the Text.*)

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INTRODUCTION AND ACKNOWLEDGMENTS

Notes have already been published on the animals occurring on the unfelled and unburnt parts of Oxshott Heath (see this JOURNAL, **12**, 1924, pp. 291-2, 299-301, 304-5). The following account gives the results of a primary survey of the animals of the felled and burnt parts of the Common made in 1922-5. In such a survey identification of specimens is a large part of the work, and I have much pleasure in acknowledging assistance in identification given as follows: Coleoptera, Commander J. J. Walker and Mr J. Collins; Hymenoptera and Diptera, Mr A. H. Hamm; Micro-lepidoptera, Mr E. G. R. Waters; Aphides, Mr F. Laing; Spiders, Dr A. R. Jackson. Dr Jackson, in particular, has named every spider I have captured. Mr W. J. Lucas has also been kind enough to allow me to use some of his notes. Even with all this help, it will be seen that certain groups (e.g. parasitic Hymenoptera) have been more or less neglected.

In the lists given in the paper, the groups of animals are always arranged in the same way; within each group the genera are arranged alphabetically and it is hoped that this may allow those who are interested in some of the groups only to extract the information they require more easily.

This paper cannot pretend to give the same amount of information about the succession of animal communities after felling as has been given in the

case of the plants¹. Animal ecology, however, has been so much neglected in England that it was thought that any information about the animals would be useful in an area where the plants had been studied and where the vegetational seres identified are easily recognised elsewhere, especially since the plants must in any case be studied first.

Although the succession of the animals has not been studied in detail, yet a certain amount of information on this subject has been obtained. Animal succession is probably of a different nature to plant succession. In the latter, as a general rule, dispersal mechanisms are good enough to allow all the candidates for a bare area to arrive fairly soon, and succession consists in the replacing of one dominant by another as the conditions become suitable for the various dominants. In the case of animals, however, where dominance does not exist, the species in a particular habitat tend to form communities attached to particular plants by a chain of food relations. In each case there are some small animals eating the plant and from that starting point there is a series of carnivores and parasites, the former of gradually increasing size. Such communities, of course, have many species in common and the largest carnivore, which may perhaps be a hawk, will be at the end of a large number of food chains leading to different plant associations.

Animal succession then comes to mean changing the food chain attached to one dominant into another attached to its successor. To show this change accurately, the alterations in a definite quadrat would have to be recorded; but in the case of the animals time was not available for such detailed work. It has, however, been found that when a new dominant arrives, most of the fauna attached arrives within a year or two, and that sometimes the change in the fauna may be very complete and rapid.

In many cases it has been found that the animal community has been slowly changing while the plant community has shown no comparable change. Thus during the colonisation of bare ground by *Calluna*, while *Calluna* spends several years in growing together to form a continuous carpet, the animal fauna is changing not only in its abundance but in its constituent species. The main factor responsible for this change is the gradual arrival of species with imperfect means of dispersal, though habitat changes may sometimes play a part as well. This lag in the occupation of suitable territory is, of course, shown in plants as well, but is probably rarely so marked as it is in animals. In the case of animals it becomes necessary as a consequence to make very careful comparative studies before the real causes of changes in the communities can be detected.

The final arrangement of animals in chains leading to particular plants requires much more knowledge of the food habits than exists at present. The data for Oxshott are very incomplete and most of the foods given for the animals are taken from text books rather than discovered by observations on

¹ See the immediately preceding paper in this issue, pp. 203-243.

the spot. This applies especially to the carnivores, the details of whose food habits are most in need of study.

It seems to be true that, as a general rule, animals are attached to plants by some sort of food relation rather than by the need of similar habitat conditions. No doubt many examples can be given of animals whose distribution is controlled by definite edaphic or physiological requirements, but probably these are usually the species which, though highly characteristic of an association, are not the most common animals in it. The commonest animals in a plant community are often those most common elsewhere. Thus, in this account, all the animals associated with a plant dominant are treated together, though the plant may be growing in what, from the point of view of plant ecology, are several habitats. An animal community may also occur in very small areas owing to the presence of the plant with which it is associated, and areas which botanically speaking are fairly homogeneous and represent a definite plant community may contain several fairly distinct animal communities.

The divisions used here are to a great extent those described and defined in "Studies on the Ecology of English Heaths," Parts I and II (this JOURNAL, **12**, 1924, p. 287 and **14**, 1926, p. 203), dealing with the plant ecology of the district.

1. DRY SERIES

A. BARE AREAS.

There are a number of animals that are characteristically found on bare sand. The most typical are the sand wasps, the fly *Anthrax*, and the tiger beetles, which often fly up as one walks across the Common. Normally such species inhabit paths, sandpits, etc., but at Oxshott there has been a great extension of their habitat. Few of the species live entirely on the bare areas, since most have to obtain their food from various plant communities, but many are controlled by the amount of bare sand available for nesting sites. A thick layer of humus usually makes a bare area unacceptable, so that for many species it is only the steeper slopes and the places where the humus has been burnt or blown away that are used. Since this community is merely an association of forms with similar nesting requirements, there is no regular food-cycle amongst its members. The species in Table I occur on dry, bare areas all over Oxshott Common, except in the pinewood which is too shady for most of them. Not enough data are available to determine the rates at which different species colonise new areas. The list of the bees and wasps includes only the most abundant species; it is hoped that this group will be more fully dealt with in a later paper.

Table I. *Animals of bare sand.*

	<i>Species</i>	<i>Food</i>	<i>Nesting place or other habitat</i>
Bee	<i>Andrena argentata</i> Sm.	Pollen and nectar (<i>Calluna</i>)	Nests in flat, hard sand
"	<i>A. dorsata</i> K.	" " (<i>Rubus</i> , <i>Epilobium</i>)	" " "
"	<i>A. fulva</i> Schr.	Pollen and nectar (<i>Salix</i>)	" " "
"	<i>A. fuscipes</i> K.	" " (<i>Calluna</i>)	" " "
"	<i>A. gwynana</i> K.	" " (<i>Salix</i>)	" " "
"	<i>A. ovatula</i> K. (afzeliiella)	" " (<i>Rubus</i>)	" " "
"	<i>A. sericea</i> Schr.	" "	" " "
Digger wasp	<i>Cerceris arenaria</i> L.	Weevils	Nests in sandy slopes
"	<i>C. labiata</i> F.	"	" " "
"	<i>C. ryhyensis</i> L.	Small bees	Nests in sandy cliffs
"	<i>Ceropales maculata</i> F.	A parasite of <i>Psammochaeres</i>	" " "
Bee	<i>Colletes succinctus</i> L.	Pollen and nectar (<i>Calluna</i>)	Nests in flat sand especially paths
Digger wasp	<i>Crossocerus wesmaeli</i> Vid.L.	Flies	Nests in cliffs and slopes
"	<i>Diodontus minutus</i> F.	Aphides	Nests in sandy cliffs
"	<i>Evagetus bicolor</i> Lep.	Spiders	Nests in flat sand
Ant	<i>Formica fusca</i> L.	Insects and secretions of aphides	Nests mainly under pine bark
Digger wasp	<i>Gorytes quadrifasciatus</i> F.	Homoptera	Nests in flat sand, or humus
"	<i>G. tumidus</i> Pz.	"	?
Bee	<i>Haliectus flavipes</i> F.	Pollen and nectar (<i>Calluna</i> , <i>Erica</i> , <i>Rubus</i>)	?
"	<i>H. minutus</i> Zett.	Pollen and nectar	Nests in sandy cliffs
"	<i>H. morio</i> F.	" "	" " "
"	<i>H. prasinus</i> Sm.	" " (<i>Calluna</i> , <i>Erica</i>)	Nests in flat sand
"	<i>H. punctatissimus</i> Sch.	Pollen and nectar (<i>Ulex</i> , <i>Rubus</i>)	?
"	<i>H. rubicundus</i> Chr.	Pollen and nectar (<i>Calluna</i> , <i>Rubus</i>)	Nests in flat sand
"	<i>H. villosulus</i> K.	Pollen and nectar (Yellow composites)	" "
Ruby wasp	<i>Hedychridium minutum</i> Lep.	Parasite of digger wasps	" "
Bee	<i>Megachile circumcincta</i> Lep.	Nectar and pollen (<i>Rubus</i>)	Nests in flat sand
"	<i>M. maritima</i> K.	" " (<i>Rubus</i> and <i>Lotus</i>)	" "
Digger wasp	<i>Mellinus arvensis</i> L.	Flies	Nests in flat sand (and cliffs)
"	<i>Methoca ichneumonides</i> Latr.	Parasite of tiger beetles	" "
"	<i>Miscophus concolor</i> Dahlb.	Small spiders	Nests in flat sand
"	<i>Myrmosa melanocephala</i> F.	Parasite of other aculeates	" "
Bee	<i>Nomada rufipes</i> F.	Parasite of <i>Andrena fuscipes</i>	" "
"	<i>N. signata</i> Pz.	Parasite of <i>A. fulva</i>	" "
Ruby wasp	<i>Notozus panzeri</i> F.	Parasite of <i>Psen</i>	" "
Digger wasp	<i>Nyssus dimidiatus</i> Jur.	Probably parasite of <i>Gorytes tumidus</i>	" "
"	<i>N. interruptus</i> F.	Probably parasite of <i>G. quadri-fasciatus</i>	" "
"	<i>Oxybelus uniglumis</i> L.	Flies	Nests in flat sand
"	<i>Priocnemis parvulus</i> Dahlb.	Spiders	Nests in flat sand (also humus)
"	<i>Psammochaeres chalybeatus</i> <i>Schiodte</i>	"	Nests in flat sand
"	<i>Ps. fuscus</i> L. (<i>viaticus</i>)	"	Nests in flat sand and slopes
"	<i>Ps. nigerrimus</i> Scop.	"	Nests in flat sand
"	<i>Ps. pectinipes</i> V.deLind.	Parasite of its congeners	" "
"	<i>Ps. plumbeus</i> F.	Spiders (esp. <i>Trochosa</i>)	Nests in flat sand and slopes
"	<i>Ps. rufipes</i> L.	"	Nests in flat sand
"	<i>Psen shuckardi</i> Wesm.	Homoptera	Nests in flat sand and cliffs

Table I (continued).

	<i>Species</i>	<i>Food</i>	<i>Nesting place or other habitat</i>
Bee	<i>Saropoda bimaculata</i> Pz.	Pollen and nectar (<i>Erica</i> , <i>Rubus</i> , <i>Epilobium</i>)	Nests in flat sand
"	<i>Sphecodes affinis</i> v.Hag.	Parasite of <i>Halictus</i>	
"	<i>S. gibbus</i> L.	"	
"	<i>S. divinus</i> K. (similis)	"	
Digger wasp	<i>Sphex</i> (<i>Ammophila</i>) <i>campestris</i> Latr.	Caterpillars (birch)	Nests in flat sand
"	<i>S. (A.) sabulosa</i> L.	" (birch and <i>Calluna</i>)	" "
"	<i>Tachysphex pectinipes</i> L.	Grasshoppers	" "
"	<i>T. unicolor</i> Pz.	"	" "
DIPTERA			
Fly	<i>Anthrax fenestratus</i> Fall.	Parasite of grasshoppers	Adult sits on bare ground
"	<i>Miltogramma punctatum</i> Mg.	Parasite of <i>Colletes</i>	
"	<i>Paragus tibialis</i> Fall.	? Perhaps a parasite	Associates with small aculeates
"	<i>Sciapus loewi</i> Beck.	Larva subterranean and probably carnivorous	Adult often in rabbit holes
"	<i>Sphixapata conica</i> Fall.	Parasite of <i>Mellinus</i> and probably of other digger wasps	
LEPIDOPTERA			
Moth	<i>Salebria fusca</i> Hw.	Larva on <i>Erica</i>	On burnt areas
COLEOPTERA			
Dung beetle	<i>Aphodius tristis</i> Pz.	Larva and adult on dung	? Associated with rabbits
Beetle	<i>Bombidium lanpros</i> Hbst.	Carnivorous	Trapped in rabbit holes
"	<i>Byrrhus fasciatus</i> F.	?	
Tiger beetle	<i>Cicendela campestris</i> L.	Carnivorous	
"	<i>C. silvatica</i> L.	"	
Dor beetle	<i>Geotrupes pyrenaeus</i> Charp.	Dung	Associated with rabbits
"	<i>G. typhoeus</i> L.	"	
Beetle	<i>Metabletus forcola</i> Gyll.	Carnivorous	
"	<i>Microzoum tibiale</i> F.	?	
HEMIPTERA			
Bug	<i>Zierona coerulea</i> L.	? Carnivorous	Associated with burnt areas
ORTHOPTERA			
Grasshopper	<i>Tettix bipunctatus</i> L.	Herbs	Flat places, mostly damper parts
ACARINA			
Mite	<i>Erythraeus regalis</i> C.L.K.	? Carnivorous	
ARACHNIDA			
Spider	<i>Aelurillus insignitus</i> Cl.	Carnivorous	
"	<i>Lycosa lugubris</i> Walck.	"	
"	<i>L. monticola</i> C.L.K.	"	
"	<i>L. nigriceps</i> Thor.	"	
"	<i>L. pullata</i> Clerck.	"	
"	<i>L. tarsalis</i> Thor.	"	
"	<i>Tarentula barpipes</i> Sund.	"	
"	<i>Trochosa picta</i> Hahn.	"	Lives in burrows in the sand
OPIOLIONIDA			
Harvestman	<i>Oligolophus tridens</i>	Carnivorous	
"	<i>Mitopus morio</i> F.	"	
MAMMALIA			
Rabbit	<i>Oryctolagus cuniculus</i> L.	Short plants	Mainly burrows in bare areas. Penetrates the pinewood with its dung beetles

B. CALLUNETUM.

The animal community associated with *Calluna* is a very definite one, and seems to be mainly controlled by the plant rather than by any special edaphic or physiological conditions. Thus the fauna of *Calluna* in woods, in damp places, and in dry, burnt or unburnt areas, is very similar, particularly as regards the most abundant species. *Erica cinerea* and *E. tetralix* seem also to support practically the same set of animals, but probably more accurate observations would show differences. The description of the animal community associated with *Calluna* at Oxshott presents certain difficulties which are met with to some extent in the study of all the communities on the Common. The older, more or less permanent areas of Callunetum have been much interfered with by man and many typical animals are rare or absent. Many of these, however, occur in the now extensive new areas of *Calluna*, and the list in Table II is made by combining the records. Obviously there is a great danger of recording as Callunetum animals those which really only occur in the early stages of colonisation. Probably further study, especially in other districts, would show which species were primarily pioneers. Many species have been found only in the older Calluneta and these may be absent from the newer areas for a number of reasons. First it is very difficult to be certain that the observations have been complete enough; many forms are difficult to find even when common, and many only occur as adults during a short part of the year. There are, however, two factors which are universally important, namely, the effect of the varying powers of dispersal and of different edaphic needs.

(1) *Dispersal*. A number of *Calluna* insects are unable to fly (usually owing to secondary loss of wings) and these do not occur as a rule in early stages of colonisation. The beetles *Helops striatus* Fourc. and *Carabus catenulatus* Scop. are exceptions. Both are wingless, yet the former is always one of the earliest arrivals on a burnt area. The *Carabus* is well known to walk about a lot in the night and owing to its large size covers the ground quickly. The following wingless insects only occur in the older Callunetum including isolated patches in the felled area which escaped burning and represent slight openings in the old pinewood: the beetles *Othius myrmecophilus* Kies., *Strophosomus coryli* F., *S. lateralis* Pk.; and the Leaf hopper *Ulopa reticulata* F. The last two species are common on most heaths, feeding on *Calluna*. Other forms are probably too small to fly far, except under favourable circumstances, e.g. the beetle *Hypocyrtus longicornis* Pk. and the fly *Limosina* spp. Where trees were growing before the fire a few species escaped by crawling up the trees. Probably this was the case with the woodlouse *Philoscia muscorum* Scop. which occurs under *Calluna* in the older areas and also under bark of burnt chestnut in parts of the Molinietum. In the same way escaped the larvae of a wingless moth, *Luffia ferchaultella* Stph. which fed on the lichens on the trunks.

(2) *Edaphic conditions*. There are many other species which are only found on older Calluneta but for whose distribution no definite reason can be given. These species are given in Table III. The newer areas lack the dense, moist moss carpet that is found in well developed Calluneta and this must have an important effect on many species. Thus the mollusc *Polita radiatula* Alder only occurs in the moss, and beneath it the slugs lay their eggs. When *Betula* grows up its leaves form an equally good cover for slugs' eggs.

In woods near Oxford many of the larger Staphylinid beetles (*Ocypus*, *Quedius*, *Philonthus*) are commonly found hibernating under moss in winter, often in very large numbers. Such beetles only occur at Oxshott on the Calluneta with moss, and this may be the controlling factor. Other insects, e.g. larvae of Syrphid flies and sawflies pupate under moss and might be similarly controlled. The species of spiders have very good powers of dispersal so that anomalies in their distribution ought mainly to be due to edaphic conditions. It will be seen that in the genera *Leptyphantes*, *Centromerus* and *Walchenaera* some species have not been found on the new areas, and these may be controlled by the edaphic conditions.

The beetles of the genus *Bradycellus* have a curious distribution. An isolated specimen of *B. verbasci* Duft. was found in the Molinietum. The Callunetum species are *B. harpalinus* Dj. and *B. similis* Dj. The former is mainly a pioneer which disappears or becomes rare in the later stages, while the latter is not uncommon in any Callunetum but does not colonise quickly. The following are the data for the two species.

In the old heather on the south ridge *B. harpalinus* is rare, while *B. similis* is often common, especially in winter. In the new areas in 1922 and 1923 (i.e. for two years after the fire) only *B. harpalinus* occurred, and it was very abundant under *Calluna*. It also occurred commonly under charred pine bark, where *B. similis* is never found. The isolated relict areas of *Calluna* probably contained *B. similis* in 1922-3, and in early 1924 *B. similis* was the commoner of the two there. On these areas their numbers are now about equal. In like manner *B. similis* appeared under the new *Calluna* in 1924 and seems now to have become the commoner species. Under *Calluna* on the damper areas *B. similis* seemed to arrive earlier. Apparently *B. harpalinus* is the best coloniser (both have well developed wings) while *B. similis* needs the damper conditions which, when the moss carpet is continuous, drive out *B. harpalinus*.

The detailed changes which result from a colonisation by *Betula* have not been recorded. There is certainly a stage when the two communities are present in alternating patches. A few notes have been made on the effect of *Betula* leaves on the *Calluna* fauna. Certain forms, e.g. *Stenus geniculatus* Gr. and *Amphigynus piceus* Marsh, are normal inhabitants of *Calluna* in the early stages of invasion. The latter beetle has not been found at Oxshott, perhaps because it is wingless, but it occurs on other London heaths. The dead leaves

also favour mollusca, allowing them to lay their eggs in a damp situation. Some of the birch-feeding larvae may be found pupating under neighbouring *Calluna* bushes. Probably most of the birds seen on the new *Calluna* areas really nest in the invading birches. A moth, *Acidalia interjectaria* B., also seems to be characteristic of the scrub stage of invasion, especially in hollows.

The general habitat of most of the *Calluna* animals is on the ground beneath the bushes of heather. Nearly all moths hide in the bushes by day and can be beaten out. The exact habitats of the species in this list will therefore not always be given. There is a separate list of the flower visitors to *Calluna*, and to the species of *Erica*. Except when the heather is in flower, the animals are not at all conspicuous; nearly all the small forms, which hide under heather, are not conspicuous even when abundant.

Table II. *Animal community of typical Callunetum (except forms only found on long established areas).*

	Species	Food	Habitat
HYMENOPTERA			
Wasp	<i>Eumenes coarctata</i> L.	Feeds larva on caterpillars	Makes a mud nest on heather
Ant	<i>Formica fusca</i> L.	Insects and secretions of aphides	Nests mainly under pine bark
Digger wasp	<i>Miscophus concolor</i> Dahlb.	Heath spiders (<i>Stemonyphantes</i>)	Nests in bare sand
Ant	<i>Myrmica ruginodis</i> Nyl.	Insects and secretions of aphides	Nests under <i>Calluna</i> or pine bark. Especially damper parts
"	<i>M. scabrinodis</i> Nyl.	Insects and secretions of aphides	As above but in dry places
"	<i>M. sulcinodis</i> Nyl.	Insects and secretions of aphides	Nests under pine bark in dry places
Wasp	<i>Vespa vulgaris</i> L.	Heather insects	Nests in scrub and wood areas
DIPTERA			
Fly	<i>Aphiochaeta pulicaria</i> Fall.	Larva a scavenger	
"	<i>A. mallochii</i> Wood	Larva "	
"	<i>Chaetoneurophora curvinnervis</i> Beck	Larva on carrion	The species may be associated with rabbits
"	<i>Cryptolucilia caesarion</i> Mg.	Larva a scavenger	Adult under heather in winter
"	<i>Enoplopteryx ciliatocosta</i> Ztt.	Larva carnivorous	Adult under heather in winter
"	<i>Euaresta conjuncta</i> Lw.	Larva on some undetermined plant	Adult under heather in winter
"	<i>Gonia ornata</i> Mg.	Parasite of <i>Agrotis</i>	Adult flies in early spring
"	<i>Machimus atricapillus</i> Fall.	Larva and adult carnivorous	
"	<i>Oscinis</i> spp.	Larva on grasses	Adult under <i>Calluna</i> in winter
"	<i>Phaonia signata</i> Mg.	Larva ? scavenger	Adult under <i>Calluna</i> in winter
"	<i>Scatella stagnalis</i> Fall.	?	
"	<i>Scatophaga stercoraria</i> L.	Larva ? scavenger	Adult carnivorous mainly in summer
"	<i>Sciara</i> sp.	" "	Adult under <i>Calluna</i>
"	<i>Sepsis</i> , at least 2 spp.	" "	
Hover fly	<i>Sphaerophoria scripta</i> L.	Larva on aphides	Adult on flowers
Crane fly	<i>Tipula</i> spp.	Larva subterranean	
Fly	<i>Wagneria lugens</i> Mg.	Parasite of noctuid caterpillars	Adult runs about on bare ground in Sept.

Table II (continued)

	<i>Species</i>	<i>Food</i>	<i>Habitat</i>
	LEPIDOPTERA		
Moth	<i>Acidalia straminata</i> Tr.	Larva on herbs	
"	<i>Agrotis pronuba</i> L.	"	Adult hides in <i>Calluna</i>
"	<i>A. tritici</i> L.	"	Adult visits <i>Calluna</i>
"	<i>Amphisbatis incongruella</i> Stt.	Larva on <i>Calluna</i>	Flies in early spring
"	<i>Anarta myrtilli</i> L.	"	Adult visits <i>Calluna</i> flowers
"	<i>Aristotelia ericinella</i> Dup.	"	
"	<i>Coleophora juncicolella</i> Stt.	"	
"	<i>Crambus culmellus</i> L.	Larva on grasses	Perhaps only a pioneer
"	<i>C. geniculeus</i> Hw.	"	" " "
"	<i>Ematurga atomaria</i> L.	Larva on <i>Erica</i> and Legu- minosae	
"	<i>Eupithicia nanata</i> Hb.	Larva on <i>Calluna</i> and <i>Erica</i>	
"	<i>Gelechia affinis</i> Dgl.	Larva on mosses	Adult hides in <i>Calluna</i>
"	<i>G. ericetella</i> Hb.	Larva on <i>Calluna</i> and <i>Erica</i>	
"	<i>G. umbrosella</i> Z.	Larva ? on mosses	Adult hides in <i>Calluna</i>
"	<i>Lasiocampa quercus</i> L.	Larva on <i>Calluna</i> and various trees	
"	<i>Phoxopteryx</i> (<i>Ancylis</i>) <i>uncana</i> Hb.	Larva on <i>Erica</i> and birch	Commoner on damp parts
"	<i>Pleurota bicostella</i> Cl.	Larva on <i>Erica</i>	
"	<i>Plusia gamma</i> L.	Larva on herbs	
"	<i>Plutella maculipennis</i> Curt.	"	
"	<i>Pterophorus monodactylus</i> L.	"	Hibernates in <i>Calluna</i>
"	<i>Salebria fusca</i> Hw.	Larva on <i>Erica</i>	
"	<i>S. palumbella</i> F.	Larva on <i>Calluna</i>	
"	<i>Scythris grandipennis</i> Hw.	Larva on <i>Ulex</i>	
"	<i>S. variella</i> Stph.	Larva on <i>Calluna</i> and <i>Erica</i>	Adult hops about on bare ground
	COLEOPTERA		
Beetle	<i>Amara famelica</i> Zimm.	Carnivorous	Perhaps only a pioneer
"	<i>A. familiaris</i> Duft.	"	Especially damper parts
"	<i>Anthicus antherinus</i> L.	Scavenger	
"	<i>Bradycellus harpalinus</i> Dj.	Carnivorous	Newer areas
"	<i>B. similis</i> Dj.	"	Older areas
"	<i>Calathus melanocephalus</i> L.	"	Perhaps more abundant where birch invades
"	<i>Carabus catenulatus</i> Scop.	Carnivorous (worms and snails)	
"	<i>Coccinella 7-punctata</i> L.	Aphides, etc.	
"	<i>C. 11-punctata</i> L.	"	
"	<i>Cryptocephalus fulvus</i> Goez.	<i>Rumex acetosella</i>	Adult hibernates under <i>Calluna</i>
"	<i>Helops striatus</i> Fourc.	Larva carnivorous under <i>Calluna</i>	Adult in nearly all habitats
"	<i>Metabletus foveola</i> Gyll	Carnivorous	
"	<i>Mycetoporus splendens</i> Marsh	"	Perhaps where birch invades
"	<i>Notiophilus biguttatus</i> F.	"	Especially in wet places
"	<i>Olisthopus rotundatus</i> Ph.	"	Does not arrive for two years
"	<i>Quedius boops</i> Gr.	"	
"	<i>Simplocaria semistriata</i> F.	?	
"	<i>Stenus atratulus</i> Er.	Carnivorous	Damper places
"	<i>S. geniculatus</i> Gr.	"	When <i>Betula</i> invades
"	<i>S. rogeri</i> Kr.	"	Damper places
"	<i>Tachyporus chrysomelinus</i> L.	Carnivorous	
"	<i>T. hypnorum</i> F.	"	
"	<i>Xantholinus linearis</i> Ol.	"	
	HEMIPTERA		
Bug	<i>Coranus subapterus</i>	Carnivorous	
"	<i>Cymus melanocephalus</i> Fieb.	?	

Table II (*continued*).

	<i>Species</i>	<i>Food</i>	<i>Habitat</i>
		HEMIPTERA	
Bug	Macrodoma micropterum Curt.	?	
"	Nabis ericetorum Schltz.	Carnivorous	
"	Orthotylus ericetorum Fall.	Calluna and Erica	
"	Scolopostethus decoratus Hhn.	?	
"	Trapezonotus arenarius L.	?	
"	Triphleps nigra Wolff.	? Carnivorous	
Leafhopper	Acócephalus albifrons L.	? Calluna	
Psyllid	Rhinocola ericae Curt.	Calluna and Erica	
Mealy wing	Aleyrodid ? sp.	Vegetarian	Very abundant under Calluna
		COLLEMBOLA	
Springtails	Collembola (unidentified)	Very abundant, vegetarian	
		THYSAMIRA	
	Campodea sp.	Vegetarian	
		ORTHOPTERA	
Grasshopper	Gomphocerus maculatus Thunbg.	Herbs	
"	Metriopectera brachyptera L.	"	Mainly damper places
"	Tettix bipunctatus L.	"	
		ARACHNIDA	
Spider	Centromerus concinnus Thor.	Carnivorous	
"	Leptyphantus tenuis Bl.	"	
"	Mangora acalypha Walck.	"	Damper places
"	Pisaura mirabilis Clerch.	"	
"	Stemonyphantus lineatus L.	"	
"	Tarentula barbipes Sund.	"	
"	Walckenaera nudipalpis Westr.	"	Damper places
"	Wideria antica Wid.	"	
"	Xysticus cristatus Clerck.	"	
		OPILIONIDA	
Harvestman	Phalangium opilio L.	Carnivorous	
		ACARINA	
Mite	Erythraeus regalis C.L.K.	Carnivorous	Under Calluna and on bare soil
		CRUSTACEA	
Woodlouse	Porcellio scaber Latr.	Scavenger and carnivorous	Newer areas
		CHILOGNATHA	
Centipedes		Carnivorous	
		DIPLOPODA	
Millipedes		? Scavengers	
		ANNELIDA	
Earthworm		Vegetarian	Damper parts of felled areas
		REPTILIA	
Grass snake	Tropidonotus natrix L.	Carnivorous	Damper parts
		AVES	
Yellow Hammer	Emberiza citrinella citrinella L.	Chiefly plants	
Partridge	Perdix perdix perdix L.	Chiefly plants, insects more in summer	
Stonechat	Saxicola torquata hibernans Hart.	Mainly insects	
		MAMMALIA	
Rabbit	Oryctolagus cuniculus L.	Herbs and Ericaceae	

Table III. *Species found only on older Callunetum.*

1 = Older *Calluna*. 2 = Pinewood, *Calluna* and *E. tetralix*. 3 = Relict *Calluna* in felled areas.

Ant	Acanthomyops alienus Först. 1	Insects and secretions of aphides	Nests in sand
„	A. umbratus Nyl. 1	Insects and secretions of aphides	Nests under <i>Calluna</i> and moss
„	Myrmica lobicornis Nyl. 1, 3	Insects and secretions of aphides	Nests under <i>Calluna</i>
LEPIDOPTERA			
Butterfly	Lycæna aegon Schiff. 1	Larva on <i>Erica</i> and <i>Orni-</i> <i>thopus</i>	Abundant on older <i>Calluna</i>
DIPTERA			
Fly	Limosina luteilabris Rdi. 1, 2	? Scavenger	Adults under moss
„	Sphaerocera subsaltans F. 1	„	
COLEOPTERA			
Beetle	Amara lunicollis Schiod. 1, 3	Carnivorous	
„	A. trivialis Gyll. 1	„	
„	Astilbus canaliculatus F. 1	Ants	
Ladybird	Chilocorus similis Ross. 1	? Aphides	
Beetle	Hypocyrtus longicornis Pk. 2, 3	? Scavenger	? Too small to fly far
„	Lochmæa suturalis Th. 1, 2	<i>Calluna</i> and <i>Erica</i>	
„	Nebria brevicollis F. 2, 3	Carnivorous	
„	Ocyptus cupreus Ross. 1	„	
„	O. olens Müll. 1	„	
„	Othius myrmecophilus Kies. 2 (3?)	?	Wingless
„	Philonthus marginatus F. 1	Carnivorous	
„	P. politus F. 1	„	
„	Quedius molochinus Gr. 3	„	
„	Q. nigriceps Kr. 2	„	
„	Sipalia circellaris Gr. 1, 2	? Carnivorous	
„	Strophosomus coryli F. 1, 2, 3	Vegetarian	Wingless
„	S. lateralis Pk. 1, 2, 3	<i>Calluna</i> and <i>Erica</i>	„
HEMIPTERA			
Leafhopper	Dicraneura variata Hardy 1	Vegetarian	
„	Ulopa reticulata F. 1, 2, 3	<i>Calluna</i>	Wingless
ORTHOPTERA			
Cockroach	Ectobius lapponicus L. 1, 3	? Scavenger	Short-winge
Grasshopper	Stauroderus bicolor Charp. 1, 3	Vegetarian	
ARACHNIDA			
Spider	Agroeca proxima Cambr. 1	Carnivorous	
„	Centromerus bicolor Bl. 1, 3	„	
„	C. silvaticus Bl. 1	„	
„	Cheiracanthium carnifex F. 1, 3	„	
„	Dictynna arundinacea L. 3	„	
„	Leptyphantes ericaeus Bl. 3	„	
„	Linyphia pusilla Sund. 3	„	
„	Micryphantes rurestris C.L.K. 1	„	
„	Nematognus obscurus Bl. 1	„	
„	Robertus lividus Bl. 1	„	
„	Walckenaera acuminata Bl. 1, 3	„	
OPILIONIDA			
Harvestman	Nemastomum lugubre Bl. 2	Carnivorous	
„	Oligolophus agrestis. 2	„	
„	Platybunus corniger Fr. 2	„	
CRUSTACEA			
Woodlouse	Philoscia muscorum Scop. 1, 2	? Scavenger and carnivore	
MOLLUSCA			
Slug	Eggs under moss. 1, 2	Vegetarian and scavenger	
Snail	Polita allaria Müll. 2	„	„
„	P. radiatula Alder. 1	„	„

Table IV. *Insect visitors of Calluna and Erica flowers.*Ca. = *Calluna*. Ci. = *Erica cinerea*. T. = *E. tetralix*. W. = Worker. F. = Female. M. = Male.

HYMENOPTERA			
Bee	<i>Andrena argentata</i> Sm.	F. Ca.	Cf. Table I
"	<i>A. fuscipes</i> K.	F. Ca.	
Hive Bee	<i>Apis mellifera</i> L.	W. Ca. Ci.	From " surrounding houses. Very common
Humble Bee	<i>Bombus agrorum</i> F.	W. Ca. Ci. W. F. T.	The commonest one on T.
"	<i>B. hortorum</i> L.	W. T.	
"	<i>B. jonellus</i> K.	W. Ca. W. M. Ci. W. F. T.	
"	<i>B. lapidarius</i> L.	M. Ca. M. W. F. Ci. W. T.	The commonest one on Ci.
"	<i>B. lucorum</i> L.	M. Ca. M. W. F. Ci. W. T.	Very common on Ci.: the W. bites through the corolla at least of T.
"	<i>B. ruderarius</i> Müll. (derhamellus K.)	M. W. T.	
"	<i>B. sylvarum</i> L.	F. T.	
"	<i>B. terrestris</i> L.	M. W. Ca. M. Ci. W. T.	Sometimes bites through corolla but not seen to do so here
Bee	<i>Colletes succinctus</i> L.	F. M. Ca.	Cf. Table I. An abundant <i>Calluna</i> bee.
"	<i>Halictus flavipes</i> F.	M. Ca. F. Ci.	Cf. Table I
"	<i>H. minutus</i> Zett.	M. F. Ca.	"
"	<i>H. prasinus</i> Smith	F. Ci.	"
"	<i>H. punctatissimus</i> Sch.	F. Ci.	"
"	<i>H. rubicundus</i> Chr.	M. Ca. T.	"
"	<i>Megachile maritima</i> K.	M. Ci.	"
"	<i>M. willughbiella</i> K.	M. Ci.	Cf. Table XXIX
"	<i>Nomada rufipes</i> F.	M. Ca.	Cf. Table I
"	<i>Prosopis genalis</i> Th.	F. Ci.	Cf. Table XXIX
"	<i>Saropoda bimaculata</i> Pz.	M. F. Ci.	Cf. Table I
Digger wasp	<i>Sphex</i> (<i>Ammophila</i>) <i>sabulosus</i> L.	M. Ca. Ci.	"
DIPTERA			
Fly	<i>Conops quadrifasciatus</i> DeG.	Ca.	? Parasite of Humble Bees
"	<i>Volucella bombylans</i> L.	F. Ca. T.	Commensal of Humble Bees
LEPIDOPTERA			
Moth	<i>Agrotis tritici</i> L.	Ca.	Cf. Table II
"	<i>Anarta myrtilis</i> L.	Ca. Ci.	"
"	<i>Plusia gamma</i> L.	Ca. Ci.	"

C. *EPILOBIUM ANGUSTIFOLIUM*.

A small animal community is associated with this plant wherever it grows at Oxshott; in other places where the plant is more permanent (e.g. cut down woods near Oxford) there are rather more kinds of insects attached to it.

Only one moth feeds on *Epilobium* at Oxshott, *Mompha raschkiella* Z. A single specimen was found in 1923. In 1924 it was common amongst particular patches of the plant, and in 1925 it was common throughout and locally abundant. The adult appears in July. The most important enemy of the willowherb, however, is a beetle, *Hallica oleracea* L. Two specimens were found in July 1924 in the Great Hollow. In the winter of 1924-5 the adults were found hibernating in great abundance in *Polytrichum* and *Molinia*

tufts in the damp areas. In late June 1925 the larvae were a plague on the leaves of *Epilobium*. The larva feeds on the underside and the lower leaves are attacked first. Short or young plants may be killed off, all the leaves being destroyed. On the area invaded by *Calluna*, where *Epilobium* grows to some extent in local clumps in small hollows, almost every clump was infected and at least three-quarters of the plants in each clump.

In the summer of 1924 a few plants in the Molinietum had the upper part of the flowering spike covered with a black aphid (not yet identified). This destroys the upper buds while the lower ones are in flower. Food is solicited from this aphid by the ant *Formica fusca* L. and it is eaten by the ladybirds (larva and adult) *Coccinella 7-punctata* L. and *Adalia bipunctata* L. and probably also by Syrphid larvae. The buds are also destroyed by the gall midge *Perrisia epilobii* F.Loew. which makes the buds swell up and fail to flower. These galls were common on 27. IX. 25. A spider, *Erigone dentipalpis* Wid., has been found to spin its web on *Epilobium*.

Table V. *Insect visitors of Epilobium.*

Bee	<i>Andrena dorsata</i> K.	Male. Cf. Table I
"	<i>Apis mellifera</i> L.	Worker: by far the most important visitor
"	<i>Bombus agrorum</i> F.	Workers
"	<i>B. lapidarius</i> L.	Workers
"	<i>B. lucorum</i> L.	Male and female
"	<i>B. pratorum</i> L.	Males. Only in shrub areas on the S.E. side
"	<i>B. terrestris</i> L.	Male and worker
Digger wasp	<i>Cerceris arenaria</i> L.	Male. Cf. Table I
"	<i>C. labiata</i> F.	" "
Bee	<i>Cilissa leporina</i> Pz.	Male
"	<i>Coelioxys rufescens</i> Lep.	Female. Parasite of <i>Megachile</i>
"	<i>Halictus flavipes</i> F.	Male. Cf. Table I
Ruby wasp	<i>Hedychridium minutum</i> Lep.	Cf. Table I
"	<i>Notozus panzeri</i> F.	Male. Cf. Table I
Digger wasp	<i>Psen bicolor</i> F.	
"	<i>P. unicolor</i> V.deL.	Cf. Table XXIX
Bee	<i>Psithyrus quadricolor</i> Lep.	Parasite of <i>B. pratorum</i> L. and found in the same situation
"	<i>Saropoda himaculata</i> Pz.	Male and female common
"	<i>Sphcodes divisus (similis)</i> K.	Female. Cf. Table I
DIPTERA		
Fly	<i>Catabomba pyrastris</i> L.	
"	<i>Sicus ferrugineus</i> L.	
COLEOPTERA		
Beetle	<i>Adalia bipunctata</i> L.	
"	<i>Coccinella 11-punctata</i> L.	
HEMIPTERA		
Bug	<i>Plagiognathus arbustorum</i> F.	
"	<i>Triphleps nigra</i> Wolff.	Cf. Table II

D. DECIDUOUS WOODS.

In the previous paper on Oxshott (this JOURNAL, 1924, p. 304) a few moths were recorded from the mixed deciduous wood on the eastern boundary of the felled area. This community has since been much more fully studied. The most important trees for insects are *Betula* spp., *Quercus*, *Alnus* and *Castanea*. All these have invaded the felled areas to a certain extent, though in this respect *Betula* is much the more important. *Castanea*, even when

common, has very few insects specially attached to it in England. The data are not sufficient to show the details of the colonisation of young birches by animals, so the following plan has been adopted. A special table is given of species found on four-year-old birches (6–12 ft. high) on 22. vi. 25. Fairly extensive records were made on this date, and no difference could be detected between birches growing in different plant habitats. Many of the species in this table are commonly recorded from young birches by other observers, but this may be because animals are easier to see on trees that are not too tall; no doubt, however, some are real pioneers. A second table will be given of species found on Oxshott Common connected with deciduous trees or the undergrowth of the woods they form. Lengthy as this list is, it can only contain a fraction of the species that really occur. In particular the ground fauna has hardly been examined. The insects have been found in the main in two ways. Firstly, they may be found sitting on the palings in the mixed wood. This, especially in the case of moths, gives a sort of random sample of the population of such a wood, though certain genera are never found. Secondly, by beating young birches, oaks, etc., on the felled areas. Many of the species may be found whichever method of search is employed and it is not yet possible to distinguish those that are especially pioneers. The insect visitors of certain plants, such as *Rubus* (Table XIV) or *Teucrium scorodonia* (Table XI), which are specially common in birch scrub, are given separately. Certain animals are definitely associated with older birch woods, mostly species needing tree trunks for some part of their life history. Three lists are given: Trunk feeders, shown in Table VII by a symbol; Table VIII, inhabitants of *Polyporus betulinus* which only grows on the older trees; Table IX, animals living under bark. This last habitat was greatly extended when many birches were killed by fire in 1921. *Castanea* suffered in the same way, and the bark-fauna of the two trees is given in one list.

A few remarks have already been made on the effect of birch leaves on the *Calluna* fauna. In the case of the invasion of *Molinia* the inadequate data available are given in Table X. The most important effect is that wood-mice, almost certainly *Apodemus silvaticus* (none caught), become very abundant. Mollusca become common and lay their eggs, and birch feeding insects pupate under *Molinia* tufts more or less covered with birch leaves.

Table VI. *Insects on young Betula.* 22. vi. 25.

HYMENOPTERA

Sawfly	<i>Croesus latipes</i> Vill.	Larva found
Ant	<i>Formica fusca</i> L.	Attending aphides
Digger wasp	<i>Psen shuckardi</i> Wesm.	Hunting for Homoptera
Sawfly	<i>Rhogogastera vividis</i> L.	? Food
"	Two unidentified larvae	Feeding on birch
Parasitic wasps	Braconids and Ichneumonids (e.g. <i>Hemiteles</i> spp.)	Abundant

Table VI (continued).

DIPTERA		
Fly	<i>Chelipoda melanocephala</i> F.	Carnivorous. Common on underside of leaves
"	<i>Chilosia pagana</i> Mg.	?
"	<i>Contarina betulina</i> Kieff.	Galls common. Some with a parasite (Hym.)
"	<i>Empis livida</i> L.	Carnivorous. Rare
"	<i>Gymnopternus aerosus</i> Fall.	" "
"	<i>Hilara interstincta</i> Fall.	" "
"	<i>Microchrysa polita</i> L.	?
"	Muscid flies of several kinds	Abundant
"	<i>Phalacrotophora fasciata</i> Fall.	Parasite of <i>Adalia bipunctata</i>
"	<i>Tachydromia minuta</i> Mg.	Carnivorous. Common
"	<i>T. flavipes</i> F. ?	" "
LEPIDOPTERA		
Moth	<i>Cacoecia unifasciana</i> Dup.	Deciduous trees (incl. birch)
"	<i>Coleophora fuscicornella</i> Z.	Larva on birch
"	<i>Drepana lacertinaria</i> L.	Larva found
"	<i>D. falcatoria</i> L.	"
"	<i>Eriocrania</i> spp.	Blotches in leaves very abundant
"	<i>Olethreutes betulaetana</i> Hw.	Rare. Larva on birch
"	<i>Orgyia antiqua</i> L.	Larva common on birch, etc.
"	<i>Phylloporia bistrigella</i> Hw.	Rare. Larva on birch
"	Three or four species of unidentified larvae	
COLEOPTERA		
Beetle	<i>Adalia bipunctata</i> L.	Very abundant. Mostly as larvae. Parasitised by <i>Phalacrotophora</i>
"	<i>Deporaus betulae</i> L.	Common. Birch feeder
"	<i>Luperus rufipes</i> Scop.	Abundant. Birch feeder
"	<i>Malthinus punctatus</i> F.	Carnivorous. Common
"	<i>Orchestes ruscii</i> Hbst.	Rare. Birch feeder
"	<i>Phyllobius maculicornis</i> Germ.	Common. Birch feeder
"	<i>Rhamphus flavicornis</i> Clair.	Abundant. Birch feeder
"	<i>Rhynchites harwoodi</i> Joy.	Common. Birch feeder
"	<i>R. nanus</i> Pk.	Abundant. Birch feeder
"	<i>Strophosomus coryli</i> F.	Common. Birch feeder
HEMIPTERA		
Bug	<i>Psallus betuleti</i> Fall.	Common. Birch feeder
Aphides	Unidentified, but very abundant	" "
Leafhopper	<i>Empoasca smaragdula</i> Fall.	Abundant. Birch feeder
"	<i>Oncopsis flavicollis</i> L.	" "
"	<i>O. rufusculus</i> Fieb.	Common. Birch feeder
"	<i>Typhlocyba</i> sp.	Abundant. Birch feeder

Table VII. *Deciduous wood community.*

Most of the Species recorded in Table VI are not repeated here.

* = Species characteristic of older woods

§ = Species lasting into the pinewood

HYMENOPTERA		
Digger wasp	<i>Cerceris arenaria</i> L.	Preys on weevils on oak and birch. Cf. Table I
Sawfly	<i>Croesus septentrionalis</i> L.	Larva on deciduous trees, e.g. birch
Parasitic wasp	<i>Exochilum brevicorne</i> Gr.	Parasite of caterpillars
Sawfly	<i>Penusa pygmaea</i> Kl.	Larva mines birch leaves (young birches)
Digger wasp	<i>Mellinus arvensis</i> L.	Hunts for flies. Cf. Table I
Sawfly	<i>Monophadnus albipes</i> Gmel.	Larva on birch (young birches)*
"	<i>Paururus noctilio</i> F.	Larva on birch (wood)
Digger wasp	<i>Passaloecus insignis</i> V.deL.	Hunts for aphids on oak and birch
"	<i>Psen unicolor</i> V.deL.	Hunts for Homoptera. Cf. Table
Sawfly	<i>Scelioneura betuleti</i> Klug.	Larva on birch (young birches)
Wasp	<i>Vespa germanica</i> Fab.	Nesting. Carnivorous§
"	<i>V. vulgaris</i> L.	" " §

Table VII (*continued*).

DIPTERA		
Fly	<i>Chrysopilus cristatus</i> F.	Larva carnivorous and subterranean
"	<i>Dioctria atricapilla</i> Mg.	Carnivorous
"	<i>D. hyalipennis</i> F. (flavipes)	"
"	<i>Hylos culiciformis</i> F.	"
"	<i>H. femoratus</i> Mull.	"
"	<i>Mesembrina meridiana</i> L.	Scavenger
"	<i>Medeterus truncorum</i> Mg.	Carnivorous on trunks*§
"	<i>Oedalea holmgreni</i> Ztt.	Carnivorous
"	<i>Pipunculus zonatus</i> Zett.	Parasite of Homoptera
"	<i>Platycnema pulicaria</i> Fall.	?
"	<i>Sciapus platypterus</i> Lw.	? Carnivorous
"	<i>Sphaerophoria scripta</i> L.	Larva on aphides
"	<i>Syrphus torvus</i> O.S.	" " §
"	<i>S. tricinctus</i> Fall.	" "
"	<i>Volucella pelluceus</i> L.	Commensal of wasps
LEPIDOPTERA		
Moth	<i>Acalla ferrugana</i> Tr.	Larva on birch, abundant in rolled leaves of young birches. Autumn 1925
"	<i>Acidalia aversata</i> L.	Larva on herbs§
"	<i>Aeronycta psi</i> L.	Larva on deciduous trees. Pupa under chestnut bark
Butterfly	<i>Adopaca sylvanus</i> Esp.	Larva on grasses. Adult on flowers, e.g. <i>Rubus</i>
Moth	<i>Agrotis pronuba</i> L.	Larva on herbs
"	<i>Aplecta nebulosa</i> Esp.	Larva on deciduous trees
"	<i>Argyresthia brockeella</i>	Larva on alder
"	<i>A. geodartella</i> L.	Larva on alder and birch §
"	<i>A. glaucinella</i> Z.	Larva on oak bark
"	<i>A. retinella</i> Z.	Larva on birch §
"	<i>Boarmia consortaria</i> F.	Larva on oak
"	<i>B. gemmaria</i> Brahm.	Larva on deciduous trees§
"	<i>Borkhausenia lunaris</i> Hw.	Larva on decayed wood
"	<i>Caeoccia lecheana</i> L.	Larva on deciduous trees
"	<i>C. xylosteana</i> L.	" " "
"	<i>Cabera pusaria</i> L.	" " §
"	<i>Campptogramma bilineata</i> L.	Larva on herbs
"	<i>Capua angustiorana</i> Hw.	Larva on deciduous trees
"	<i>Carcina quercana</i> F.	Larva on oak
"	<i>Chinabache fagella</i> F.	Larva on deciduous trees
Butterfly	<i>Celastrina argiolus</i> L.	Larva on holly and ivy
Moth	<i>Coleophora bicolorrella</i> Stt.?	Larva on birch and alder (young birches)
"	<i>C. lutipennella</i> Z.	Larva on oak
"	<i>Crambus pinellus</i> L.	Larva on ? grasses
"	<i>Elachista cygnipennella</i> Hb.	Larva on grasses
"	<i>Endotricha flammealis</i> Schiff.	Larva on dead leaves
"	<i>Epiblema bilunana</i> Hw.	Larva on birch catkins§
"	<i>E. similana</i> Hb.	Larva on birch (young birches)
"	<i>E. solandriana</i> L.	Larva on alder
"	<i>Eriocrania</i> sp. undescribed	Larva on birch (young birches 3-4 years)
"	<i>E. purpurella</i> Hw.	" " "
"	<i>E. salopiella</i> Stt.	" " "
"	<i>E. senipurpurella</i> Stph.	" " "
"	<i>E. unimaculella</i> Zett.	" " "
"	<i>Euchloris pustulata</i> Hufn.	Larva on oak
"	<i>Euchoeca obliterata</i> Hufn.	Larva on alder
"	<i>Eupoecilia nana</i> Hw.	Larva in catkins of birch
"	<i>Fumeca casta</i> Pall.	Larva feeds on refuse, pupates on trunks*§
"	<i>Gelechia luculella</i> Hb.	Larva on oak
"	<i>G. proximella</i> Hb.	Larva on birch
"	<i>G. umbrosella</i> Z.	Larva on mosses
Butterfly	<i>Geometra papilionaria</i> L.	Larva on deciduous trees
Butterfly	<i>Gonepteryx rhamni</i> L.	Larva on Rhamnus
Moth	<i>Gracilaria alchimiella</i> Sa.	Larva on oak
"	<i>Grapholitha ramella</i> L.	Larva on birch (young birches)
"	<i>G. trimaculana</i> Don.	Larva on elm

Table VII (continued).

LEPIDOPTERA		
Moth	<i>Hedya dealbana</i> Fröl.	Larva on sycamore
"	<i>H. ocellana</i> F.	Larva on deciduous trees
"	<i>Heliozole betulae</i> Stt.	Larva on birch (young birches)
"	<i>Incurvaria muscicella</i> F.	Larva on Rosaceae
"	<i>I. pectinea</i> Hw.	Larva on birch (young birches)
"	<i>Larentia viridaria</i> F.	Larva on galium
"	<i>Lithocolletis faginella</i> Z.	Larva on beech
"	<i>L. messaniella</i> Z.	Larva on oak
"	<i>L. quercifoliella</i> Z.	"
"	<i>L. ulmifoliella</i> Hb.	Larva on birch (young birches)
"	<i>Luffia ferchaultella</i> Steph.	Larva on <i>Lecanora varia</i> , etc., on trunks*§
"	<i>Lyonetia clerckella</i> L.	Larva on deciduous trees
"	<i>Monopis feruginella</i> Hb.	?
"	<i>Notocelia uddmanniana</i> L.	Larva on <i>Rubus</i>
"	<i>Oleuthreutes corticana</i> Hb.	Larva on birch
"	<i>O. lacunana</i> Dup.	Larva on <i>Rubus</i> , etc.
"	<i>Ornix betulae</i> Stt.	Larva on birch (young birches)
"	<i>Pandemis ribcana</i> Hb.	Larva on deciduous trees
"	<i>Paedisca corticana</i> Hb.	Larva on oak
"	<i>Phalera bucephala</i> L.	Larva on birch, etc., defoliating a young birch in VII. 23
"	<i>Salebria betulae</i> Goeze.	Larva on birch (young birches)
"	<i>Scoparia ambigalis</i> Tr.	Larva on moss. Adult hides on trunks*§
"	<i>S. frequentella</i> Stt.	"
"	<i>Swammerdamia heroldella</i> Tr.	Larva on birch. Adult hides on trunks
"	<i>Talaeoporia tubulosa</i> Retz.	Larva on lichens on trunks*§
"	<i>Tinea parasitella</i> Hb.	Larva in birds' nests
"	<i>T. semifulvella</i> Hw.	"
"	<i>Tischeria complanella</i> Hb.	Larva on oak
"	<i>Tortrix loeflingiana</i> L.	Larva on deciduous trees (young birches)§
"	<i>T. viridana</i> L.	Larva on oak
"	<i>Xenolechia humeralis</i> Z.	?
COLEOPTERA		
Beetle	<i>Athons haemorrhoidalis</i> F.	Larva on roots§
"	<i>Attelabus curculionides</i> L.	Larva on young oak
"	<i>Byturus tomentosus</i> F.	Larva in flowers of <i>Rubus</i>
"	<i>Coccinella 7-punctata</i> L.	Larva feeds on aphides§
"	<i>C. 10-punctata</i> L.	" " §
"	<i>Cryptocephalus parvulus</i> Müll.	Larva on birch
"	<i>Ernobius mollis</i> L. (agg.)	?
"	<i>Halyzia 18-guttata</i> L.	Larva on aphides§
"	<i>Hoplia philanthus</i> Füss.	Larva on roots of plants
"	<i>Luperus rufipes</i> Scop.	Birch
"	<i>Phyllobius argentatus</i> L.	Deciduous trees
"	<i>P. pyri</i> L.	" " §
"	<i>Phyllodecta vitellinae</i> L.	Larvae on aspen
"	<i>Rhagonycha fulva</i> Scop.	Predaceous
"	<i>Serica brunnea</i> L.	Larva on roots
"	<i>Strangalia armata</i> Hbst.	Larva on decaying wood
HEMIPTERA		
Bug	<i>Aetorhinus angulatus</i> Fall.	Young birches
"	<i>Anthocoris nemorum</i> L.	Aphides
"	<i>Deraeocoris ruber</i> L.	<i>Rubus</i> and various herbs
"	<i>Orthotylus flavinervis</i> Kb.	Alder
"	<i>Plagiognathus chrysanthemi</i> Wolf.	Various herbs
"	<i>P. arbustorum</i> F.	Various herbs (e.g. <i>Teucrium</i>)
Leafhopper	<i>Aphrophora alni</i> Fall.	Deciduous trees
"	<i>Batrachomorpha lanio</i> L.	Oak
Psyllid	<i>Psylla fürsteri</i> Flor.	Alder
NEUROPTERA		
Lacewing	<i>Chrysopa perla</i> L.	Larva on aphids (young birches)
"	<i>Ch. vulgaris</i> Schneider	" " "

Table VII (*continued*)

ACARINA		
Mite	Eriophyes nalepai Focken	Gall on alder
ARACHNIDA		
Spider	Epeira diadema L.	Web on young birches
AVES		
Cuckoo	Cuculus canorus canorus L.	Insects
Robin	Erithacus rubecula melophilus Hart.	"
Jay	Garrulus glandarius rufitergum Hart.	Mainly a general carnivore*§
Green Wood-pecker	Picus viridis virescens Brehm.	Ants, etc.*§
Stonechat	Saxicola torquatus hibernaus Hart.	Mainly insects
MAMMALIA		
Mouse	Apodemus silvaticus L.	(Probably) mainly herbivorous

Table VIII. *Inhabitants of Polyporus betulinus*

HYMENOPTERA		
A Proctotrupid beetle parasite		
COLEOPTERA		
Beetle	Atheta aequata Er.	? Carnivorous
"	A. cauta (parva) Er.	"
"	A. fungivora Th.	"
"	A. sericea Muls.	"
"	Cis bilamellatus Wood.	Fungus
"	Coninomus nodifer Westw.	"
"	Litargus connexus Geoff. (bifasciatus)	"
"	Octotemnus glabriculus Gyll.	"
"	Proteinus ovalis Steph.	? Carnivorous
COLLEMBOLA		
Springtail	Collembola common	Vegetarian and scavenger

Table IX.

Animals under bark of dead birches (B.), and chestnuts (C.)

DIPTERA		
Fly	Larva of Forcipomyia pallida Winn.	C. (B. ? same species). Scavenger
COLEOPTERA		
Beetle	Atheta aequata Er.	B. Scavenger
"	Cerylon histeroide F.	B. Larva carnivorous
"	Cis vestitus Mel.	B. Fungus eater
"	C. villosulus Marsh.	B. "
"	Ditoma crenata F.	B. Larva carnivorous
"	Dromius quadrinotatus Pz.	C. Carnivorous
"	Helops striatus Fourc.	C. ? Scavenger. Larva, cf. Table II
"	Homalium rivulare Pk.	C. ? Carnivorous
"	Litargus connexus Geoff. (bifasciatus)	C. B. Fungus eater
"	Melasis buprestoides L.	C. Rotten wood of deciduous trees
"	Ocupus morio Gr.	C. Carnivorous
"	Pteryx suturalis Heer.	B. Fungus eater
"	Phyllodrepa vilis Er.	C. Fungus eater? or carnivorous
"	Rhinosismus planirostris F.	C. ?
"	Rhizophagus bipustulatus F.	C. B. Carnivorous on bark beetles
"	Scolytus intricatus Ratz.	C. Wood of deciduous trees
"	Silpha atrata L.	C. ? Carnivorous
"	Silvanus unidentatus Ol.	B. Larva ? carnivorous
"	Thectura cuspidata Er.	B. Feeds on Collembola

Table IX (continued).

HEMIPTERA			
Bug	<i>Aneuris laevis</i> F.	C.	?
"	<i>Piezostethus cursitans</i> Fall.	B.	? Carnivorous
"	<i>Xylocoris ater</i> Duf.	C.	"
COLLEMBOLA			
Springtails	Collembola (unnamed) abundant	C. B.	Wood and fungus
THYSANOPTERA			
	Thrips (unnamed bark species)	C.	?
NEUROPTERA			
Snake fly	<i>Rhaphidia</i> sp.	C. B.	Larva carnivorous under bark
ARACHNIDA			
Spider	<i>Epeira umbratica</i> Clk.	C.	Lives under bark, but catches insects from outside
"	<i>Salticus scenicus</i> Clk.	C.	Hibernates under bark, in summer hunts on trunks
"	<i>Zilla atrica</i> C.L.K.	C.	Carnivorous
CRUSTACEA			
Woodlouse	<i>Philoscia muscorum</i> Swp.	C.	Scavenger and ? carnivorous
"	<i>Porcellio scaber</i> Latr.	C. B.	" "
MOLLUSCA			
Slug	<i>Arion subfuscus</i> Drap.	C. B.	Scavenger
"	<i>Limax maximus</i> L.	B.	"
Snails	<i>Polita alliaria</i> Müll.	B.	" ?

Table X. *Animals found in Molinia with dead birch leaves.*
Inner circle 26. XII. 25.

DIPTERA			
Fly	<i>Limosina moesta</i> Villen.	?	Scavenger; abundant
COLEOPTERA			
Beetle	<i>Notiophilus biguttatus</i> F.		Carnivorous
"	<i>Olophrum piceum</i> Gyll.	"	?
"	<i>Othius myrmecophilus</i> Kies.	"	?
CHILOGNATHA			
Centipede	<i>Scolopendra</i> sp.		Carnivorous. Common
CRUSTACEA			
Woodlouse	<i>Philoscia muscorum</i> Scop.		Scavenger and carnivorous. Common
MOLLUSCA			
Slugs	Eggs probably of slugs		Common
MAMMALIA			
Mouse	<i>Apodemus silvaticus</i> L. (probably)		Runs very numerous. Mainly vegetarian

Table XI. *Insect visitors of Teucrium scorodonia.*

M. = Male. F. = Female. W. = Worker

HYMENOPTERA			
Humble Bee	<i>Bombus agrorum</i> F.	W.	Common
"	<i>B. hortorum</i> L.	M.	"
"	<i>B. lapidarius</i> L.	M.	"
"	<i>B. lucorum</i> L.	M.	"
"	<i>B. rudericus</i> Müll. (<i>derhamellus</i> K.)	W.	"
Bee	<i>Saropoda bimaculata</i> Pz.	M. F.	Common
DIPTERA			
Fly	<i>Hylos culiciformis</i> F.		Cf. Table VII

E. THE GREAT HOLLOW.

In its animals, just as in its plants, this area has a special character. The greater number of the animal communities on the Common are represented in it. It is of interest to note that just as colonisation by oak, birch, and *Castanea* has proceeded further here than elsewhere, so the animals of deciduous woods are better represented. Some, such as *Scoparia* spp., are mainly typical of older woods, and others such as *Endotricha flammealis* Schiff., do not arrive, as a rule, till fairly late in succession. The peculiar character of the hollow, however, is probably most clearly seen in the greater abundance of insect life in general. This it probably owes mainly to its sheltered position, but partly to the fact that it acts as a trap to many of the smaller forms. The damp spots at the bottom of the hollow, besides allowing *Juncus* to grow, support several animals which are characteristic of the wetter areas (see Table XII).

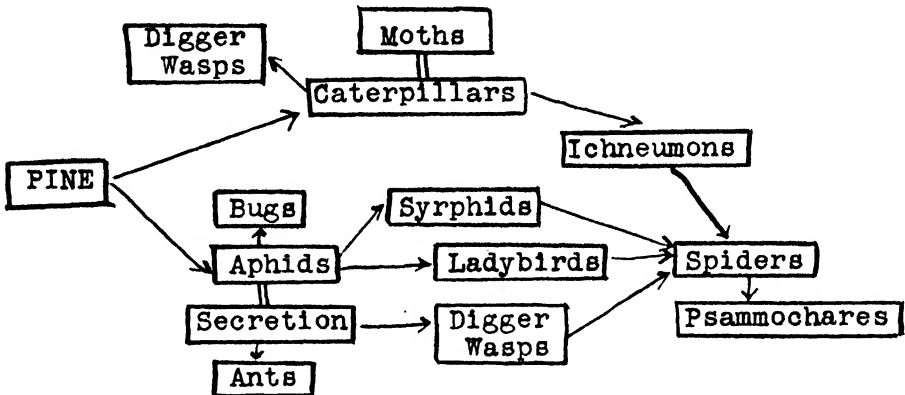


FIG. 1. Food-cycle on young pine.

At the other end of succession there has been a considerable growth of *Pinus* and a number of pine insects have been recorded. The regular pine ant, however, *Formica rufa* L. has not yet arrived. The most important herbivore on the pines is the aphid *Dilachnus pini* L. This is fed on by bugs (*Anthocoris nemorum* L.), ladybirds, and syrphid larvae. Spiders build their webs all over the pines and catch the winged individuals of the aphides, and also the adults of their enemies. The various digger wasps which visit the aphides for their secretions also get caught by the spiders. Finally digger wasps prey on the spiders. Such a community can be found on most of the young pines, even isolated ones in the damp areas, but is best developed in the Great Hollow. A rough diagram of the food relations is given in Fig. 1: the species concerned will be found in Table XIII.

Probably parasites rather than carnivores are the main check on many of the animals. But since the parasites are probably often controlled by carnivores the diagram represents a broad approximation to the truth. Thus, when

a spider is said to eat a moth, it may often eat mainly the parasites of the moth. As far as the total food supply is concerned the result is the same. The moth *Retinia* which feeds on the pine is particularly important because the larvae destroys the growing tip; if the moth were sufficiently abundant it might retard growth enough to modify or at least slow down succession.

When *Pinus* invades a birch scrub successfully a few of the birches generally survive in the pinewood. These continue to support a number of the birch insects; in Table VII such insects, still remaining in the pinewood at Oxshott, are marked with a symbol.

Table XII. *Animals typical of wetter areas which occur in the Great Hollow.*

LEPIDOPTERA		
Moth	<i>Colcophora caespititiella</i> Z.	Larva on <i>Juncus effusus</i>
COLEOPTERA		
Beetle	<i>Crepidodera ferruginea</i> Scop.	Vegetarian
"	<i>Cytillus varius</i> F.	?
HEMIPTERA		
Bug	<i>Nabis rugosus</i> L.	Carnivorous
Leathopper	<i>Philaenus lineatus</i> L.	Vegetarian
AMPHIBIA		
Toad	<i>Bufo vulgaris</i> aur. L. (?)	Young (perhaps really the Natterjack <i>B. calamita</i> Laur.)

Table XIII. *Animals on young pines in the Great Hollow.*

HYMENOPTERA		
Ant	<i>Acanthomyops niger</i> L.	Secretions of aphides
Digger wasp	<i>Crossocerus wesmæli</i> V. de Lind.	Secretions of aphides. Cf. Table I
Ant	<i>Formica fusca</i> L.	" " "
Digger wasp	<i>Oxybelus uniglumis</i> L.	" " "
"	<i>Psammochares fuscus</i> L. (viaticus) and spp.	Catches spiders for its larvae
"	<i>Psen</i> spp.	Secretions of aphides
"	<i>Sphex sabulosa</i> L.	Caterpillars, e.g. larva of <i>Panolis</i>
Bees	Various bees coming to secretions of aphides caught by spiders	
Parasitic wasps	Numerous ichneumons (unnamed) are similarly caught	
DIPTERA		
Fly	<i>Syrphus vitripennis</i> Mg. and spp.	Larva on aphides
LEPIDOPTERA		
Moth	<i>Gelechia dodecella</i> L.	Larva on <i>Pinus</i>
"	<i>Oenoserstoma piniariella</i> Z.	"
"	<i>Panolis griseovariegata</i> Goeze	"
"	<i>Retinia buoliana</i> Schiff.	"
COLEOPTERA		
Ladybird	<i>Adalia bipunctata</i> L.	Aphides
"	<i>Anatis ocellata</i> L.	"
"	<i>Coccinella 7-punctata</i> L.	"
"	<i>Exochamus quadripustulatus</i> L.	"
Beetle	<i>Myelophilus piniperda</i> L.	Burrows in shoots of <i>Pinus</i>
Bug	<i>Anthocoris nemorum</i> L.	Aphides
Aphid	<i>Dilachnus pini</i> L.	<i>Pinus</i> . (Probably there are other species of aphides)
ARACHNIDA		
Spider	<i>Agelena labyrinthica</i> Cl.	Insects. Very common in summer
"	<i>Linyphia triangularis</i> Cl.	Insects. Autumn

2. DAMP SERIES

A. AQUATIC COMMUNITIES.

The Black Pond is the only large permanent body of water on the Common and has a rich aquatic life, forming a relatively self-contained community, which, however, has scarcely been studied. The dragonflies which breed there range all over the Common, becoming more abundant as the pond is approached, so that there must be a gradient in whatever biotic effects these highly carnivorous insects produce. Most of the dragonflies recorded have been seen by me and are common; others are recorded by Lucas (1900) as common at the right time of the year. A number of other species, only occurring as strays, have not been included. The incompleteness of the records for the Black Pond is obvious in the list, where practically no food for the various carnivores is recorded. The reed swamp on the edge of the pond, also, has not been much investigated; the data for the pond and its margin are given in Tables XIV and XV. The Black Pond is of further importance in being at least the main source of insects for all the temporary pools.

These pools fall into a number of classes depending on their degree of permanence (which is usually correlated with their depth) and their distance from the Black Pond.

The shallower pools were first developed on the bare burnt soil of the Molinietum. When they dried up a dense carpet of *Funaria*, and later *Polytrichum*, was formed. If shallow pools are formed on this carpet they are unfavourable to animal life, and in any case the moss is so absorbent that there is little free water. Such pools, therefore, are a feature of early stages in succession (see Table XVI).

Deeper pools (9 in. to 2½ ft.) are much more permanent, but they may dry up completely two or three times in the course of the summer. When they dry up they are carpeted by *Juncus supinus*, not by mosses. Such pools occur throughout the Molinietum and they have quite a rich fauna, especially when situated near the Black Pond. A number of insects are able to breed in the deeper pools and not in the shallower pools. The number of kinds and individuals of insects present depends directly on the length of time since the pool was last dried up. At the end of the wet summer of 1924 they had a particularly rich fauna (see Tables XVII and XVIII).

The work of Harnisch (1925) in Germany, Wesenberg-Lund (1921) in Denmark and Johannsen (1921) in Arctic Canada, shows that the community inhabiting such pools is very similar throughout the northern palaeartic region. Wesenberg-Lund has given an interesting account of the enemies of the mosquito larvae and pupae which are one of the main links in the food chain. A very tentative and incomplete food-cycle for the pools is given in the diagram (Fig. 2). The food relations are complicated because, in the case

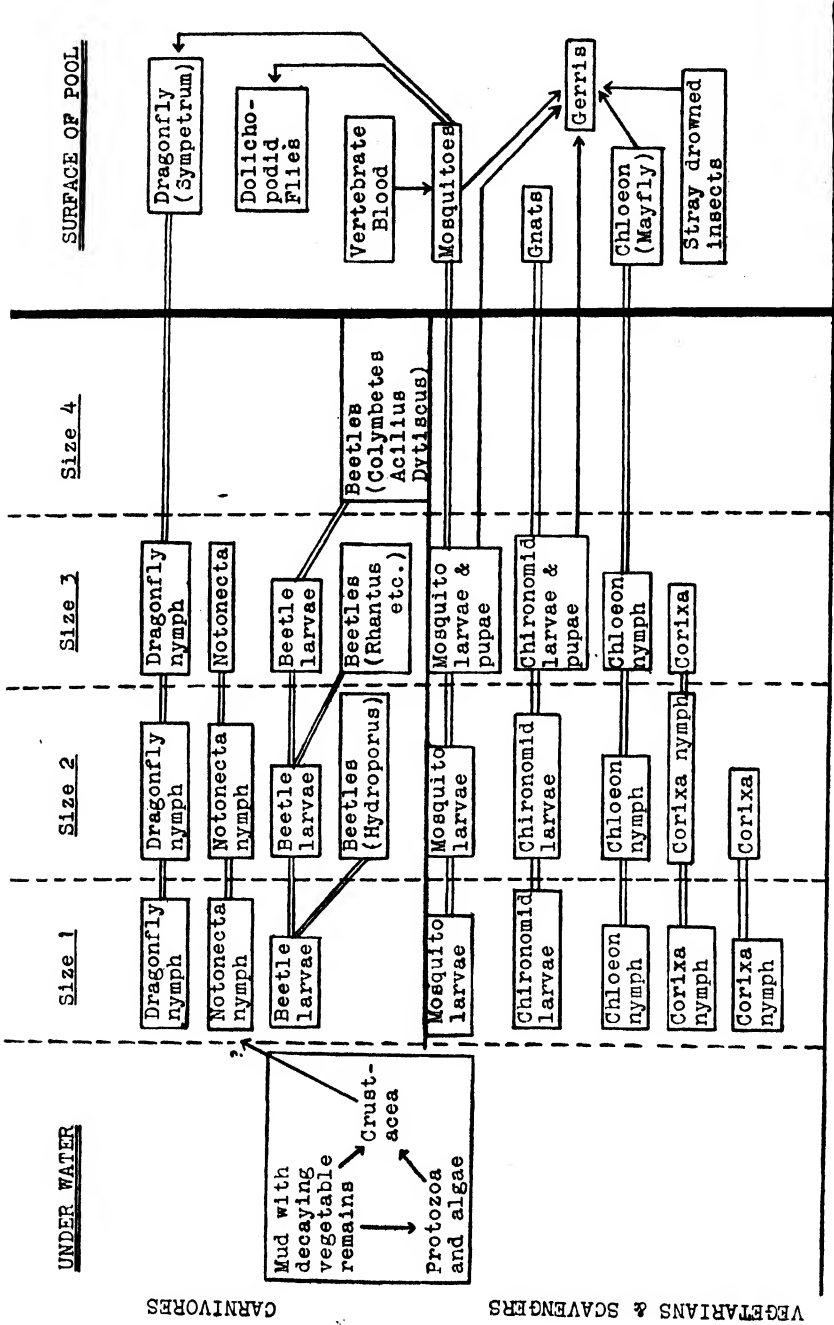


FIG. 2.

of most water beetles and other aquatic insect larvae, it is almost certain that the main factor deciding the food of the carnivore is its size. Many larvae are cannibals and will eat smaller larvae of their own species. A scheme has been adopted which attempts to show the relation of size to the food chain. Among the beetles there are three main sizes, though these are not, of course, sharply marked off, represented by *Hydroporus*, *Agabus* and *Colymbetes-Dytiscus* respectively. The largest type of larva, of course, grows through all the other sizes. In the diagram the thick vertical line represents the surface of the water. The horizontal line divides the aquatic community into carnivores and refuse-eaters. The vertical dotted lines divide the animals into four size-groups, representing either different sizes of the adults, or sizes passed through by growing larvae. The carnivores in any one size-group will eat all the carnivores smaller than themselves, and any refuse-eater up to their own size. Thus a carnivore will eat any other carnivore to the left of it in the diagram and any refuse feeder to the left of it or vertically beneath. Further investigation would probably show that specialisation exists amongst the carnivores in their choice of food and also perhaps that the largest forms would neglect the smallest food animals and only pay attention to those nearer to them in size.

Table XIV. *Animals noticed in the Black Pond.*

HEMIPTERA			
Bugs	<i>Aretocoris fabricii</i> Fieb.	Scavenger and ? partly carnivorous	
"	<i>A. hieroglyphica</i> Duf.	"	" "
"	<i>A. moesta</i> Fieb.	"	" "
"	<i>Callicorixa praeusta</i> Fieb.	"	" "
"	<i>Corixa geoffroyi</i> Leach	"	" "
TRICHOPTERA			
Caddis	<i>Phryganea varia</i> F.	Larva carnivorous	
"	Polycentropodidae ? sp.	"	" ?
ODONATA			
Dragonfly	<i>Aeschna cyanea</i> Müll.	Larva carnivorous.	Adult carnivorous above pond, etc.
"	<i>A. grandis</i> L.	"	" " "
"	<i>A. juncea</i> L.	"	" " "
"	<i>A. mixta</i> L.	"	" " "
"	<i>Agria puella</i> L.	"	" " "
"	<i>Anax imperator</i> Leach	"	" " "
"	<i>Cordulia aenea</i> L.	"	" " "
"	<i>Enallagma cyathigerum</i> Charp.	"	" " "
"	<i>Leucorhinia dubia</i> Lind.	"	" " "
"	<i>Libellula depressa</i> L.	"	" " "
"	<i>L. quadrimaculata</i> L.	"	" " "
"	<i>Pyrrosoma nymphula</i> Sulz.	"	" " "
"	<i>P. tenella</i> Vill.	"	" " "
"	<i>Sympetrum scoticum</i> Don.	"	" " "
AVES			
Moorhen	<i>Gallinula chloropus chloropus</i> L.	Mainly aquatic plants	
Coot	<i>Fulica atra atra</i> L.	"	

Table XV. *Animals in the reed swamp at the edge of the Black Pond.*

DIPTERA		
Fly	<i>Leptis scolopacea</i> L.	Larva subterranean, carnivorous. Adult carnivorous
LEPIDOPTERA		
Moth	<i>Crambus pascuellus</i> L.	Larva on grasses
"	<i>C. pratellus</i> L.	"
"	<i>C. tristellus</i> F.	"
COLEOPTERA		
Beetle	<i>Acupalpus meridianus</i> L.	Carnivorous
"	<i>Coccidula rufa</i> Abst.	"
"	<i>C. scutellata</i> Hbst.	"
"	<i>Cyphon padi</i> L.	Larva aquatic ? carnivorous
"	<i>Plectroscelis concinna</i> Marsh.	Cruciferae
AVES		
Snipe	<i>Capella gallinago gallinago</i> L.	Subaquatic insects, worms, etc.

Table XVI. *Shallow temporary pools.*

COLEOPTERA		
Beetle	<i>Agabus bipustulatus</i> L.	Carnivorous
"	<i>Helophorus affinis</i> Marsh.	? Vegetarian. This species may even occur in foot-marks
"	<i>Hydroporus melanarius</i> Stm.	Carnivorous
"	<i>H. planus</i> F.	"
"	<i>H. pubescens</i> Gyll.	Carnivorous. This species may aestivate in the dried mud

Table XVII. *Deeper temporary pools with Juncus supinus.*

DIPTERA		
Mosquito	<i>Aedes annulipes</i> Mg.	Larva vegetarian and scavenger
Gnats	Chironomids. None identified	
Fly	<i>Caenia albula</i> Mg.	? Adult on the surface
"	<i>Campsicnemus scambus</i> Fall.	Carnivorous, on the surface
"	<i>Dolichopus vitripennis</i> Mg.	" "
"	<i>Hydroporus bipunctatus</i> Lehm.	" "
"	<i>Oethera mantis</i> DeG.	" "
COLEOPTERA		
Beetle	<i>Acilus sulcatus</i> L.	Carnivorous, on the surface
"	<i>Agabus chalconotus</i> Pz.	Carnivorous (especially where there is much dead grass)
"	<i>A. bipustulatus</i> L.	Carnivorous. Very common
"	<i>Anacaena limbata</i> F.	? Vegetarian
"	<i>Berosus luridus</i> L.	"
"	<i>Colymbetes fuscus</i> L.	Carnivorous. Common
"	<i>Dytiscus marginalis</i> L.	"
"	<i>Gyrinus natator</i> Scop.	Carnivorous, on the surface
"	<i>Helochares punctatus</i> Shp.	? Vegetarian
"	<i>Helophorus affinis</i> Marsh.	"
"	<i>Hydroporus discretus</i> Fair.	? Carnivorous
"	<i>H. erythrocephalus</i> L.	"
"	<i>H. gyllenhali</i> Schiödt	Common
"	<i>H. neglectus</i> Schaum.	"
"	<i>H. planus</i> F.	"
"	<i>H. pubescens</i> Gyll.	Common
"	<i>Ibybius aenescens</i> Th.	Carnivorous
"	<i>Rhantus bistriatus</i> Berg.	"
"	<i>R. pulverosus</i> Steph.	"

Table XVII (continued)

HEMIPTERA			
Bug	<i>Arctocoris fabricei</i> Fieb.	? Scavenger and partly carnivorous.	Common
"	<i>A. fallenii</i> Fieb.	" "	"
"	<i>A. hieroglyphica</i> Duf.	" "	Common
"	<i>A. limitata</i> Fieb.	" "	"
"	<i>A. moesta</i> Fieb.	" "	Common
"	<i>A. sahlbergi</i> Fieb.	" "	"
"	<i>A. semistriata</i> Fieb.	" "	"
"	<i>A. striata</i> L.	" "	"
"	<i>Callicorixa praeusta</i> Fieb.	" "	"
"	<i>Corixa geoffroyi</i> Leach	" "	Common
"	<i>Hygrotrechus (Gerris) paludum</i> F.	Carnivorous, on the surface	"
"	<i>Limnotrechus (G.) gibbifer</i> Schum.	" "	"
"	<i>L. lacustris</i> L.	" "	Common
"	<i>L. odontogaster</i> Zett.	" "	"
"	<i>Notonecta furcata</i> F.	Carnivorous	"
"	<i>N. glauca</i> L.	" Common	"
"	<i>N. halophila</i> Edw. (<i>viridis</i> Delc.)	"	"
"	<i>N. maculata</i> F.	" Common	"
EPHEMEROPTERA			
Mayfly	<i>Chloeon dipterum</i> L.	Larva vegetarian	
ODONATA			
Dragonfly	<i>Sympetrum</i> sp.	Larva carnivorous	
ARACHNIDA			
Spider	<i>Tetragnatha</i> sp.	Carnivorous, on rushes at edge	
AMPHIBIA			
Frog	<i>Rana temporaria</i> L.	Carnivorous (not breeding here?)	

Table XVIII. *In Juncus supinus of dried pools.*

LEPIDOPTERA			
Moth	<i>Coleophora glauciolella</i> Wood	Larva on <i>Juncus</i>	
"	<i>Glyphipteryx thrasonella</i> Scop.	"	Abundant
COLEOPTERA			
Beetle	<i>Aculpalpis dorsalis</i> F.	Carnivorous	
"	<i>Bembidium lampros</i> Hbst.	"	
"	<i>Pterostichus diligens</i> Stm.	"	
"	<i>P. nigrita</i> F.	"	
HEMIPTERA			
Bug	<i>Acanthia saltatoria</i> L.	Carnivorous	
"	<i>Limnotrechus gibbifer</i> Schum.	(Aestivating)	
CRUSTACEA			
Woodlouse	<i>Porcellio scaber</i> Latr.	Scavenger and carnivorous	
ARACHNIDA			
Spider	<i>Erigone atra</i> Bl.	Carnivorous	

Another set of animals lives in the drains that were dug across the Common after felling. In the drains which are choked with dead leaves of *Molinia* the only insect that has been noted is the beetle *Agabus chalconotus* St. Many of the drains however are more like small streams and have a proper aquatic vegetation, consisting of *Glyceria fluitans*, *Polygonum polygonifolius* and much *Spirogyra*. Similar ditches on other London heaths have been found to have a nearly identical fauna (Table XIX). The edge of these drains has also a very characteristic set of animals, some of which are found nowhere else on the Common (Table XX). A number of flies with aquatic or semi-aquatic

larvae probably breed in these ditches. The adults are either flower-haunting bee-flies (*Eristalis*) or blood-suckers (Tabanids) and are found all over the Common. The species that have been recorded are given in Table XXI.

Table XIX. *Insects in the ditches.*

DIPTERA			
Fly	<i>Gymnopternus nanus</i> Meq.	Carnivorous	22
"	<i>Hydrellia griseola</i> Fall.	Larva on grasses	11
"	<i>Limosina humida</i> Hal.	?	24
"	<i>Parhydra aquila</i> Fall.	?	2
"	<i>P. coarctata</i> Fall.	?	2
"	<i>P. quadripunctata</i> Mg.	?	8
COLEOPTERA			
Beetle	<i>Agabus bipustulatus</i> L.	Carnivorous	
"	<i>A. sturmii</i> Gyll.	" Common	
"	<i>Anacaena globulus</i> Pk.	? Vegetarian	
"	<i>A. limbata</i> F.	"	
"	<i>Helophorus affinis</i> Marsh.	"	
"	<i>Hydrobius fuscipes</i> L.	"	
HEMIPTERA			
Bug	<i>Arctocoris fabricii</i> Fieb.	Scavenger and ? partly carnivorous	
"	<i>A. sahlbergi</i> Fieb.	"	
"	<i>Velia currens</i> F.	Carnivorous, on the surface	"
ODONATA			
Dragonfly	<i>Aeschna juncea</i> L. la.	Carnivorous	
"	<i>Agrioid</i> la.	"	
TRICHOPTERA			
Caddis	<i>Polycentropodidae</i> la.	Carnivorous	

Table XX. *In vegetation at the edges of ditches.*

COLEOPTERA			
Beetle	<i>Agononum oblongum</i> F.	Carnivorous	
"	<i>Bembidium lampros</i> Hbst.	"	
"	<i>Lathrobium brunnipes</i> F.	"	
"	<i>L. terminatum</i> Gr.	" Common	
"	<i>Olophrum piceum</i> Gyll.	"	
"	<i>Pterostichus minor</i> Gyll.	" Common	
"	<i>P. strenuus</i> Pz.	"	
"	<i>Stenus ossium</i> Steph.	"	
"	<i>S. rogeri</i> Kr.	"	
COLLEMBOLA			
Springtails	<i>Collembola</i> common	Vegetarian and scavengers	
CRUSTACEA			
Woodlouse	<i>Porcellio scaber</i> Latr.	Scavenger and partly carnivorous	
ARACHNIDA			
Spider	<i>Centromerus prudens</i> Cambr.	Carnivorous	
"	<i>Walckeraera nudipalpis</i> Westr.	"	

Table XXI. *Diptera with aquatic or subaquatic larvae.*

Fly	<i>Chrysops coccitons</i> L.	Larva carnivorous. Bloodsucker
"	<i>Eristalis arbustorum</i> L.	Larva scavenger. On flowers
"	<i>E. intricarius</i> L.	" "
"	<i>E. pertinax</i> Scop.	" "
"	<i>E. tenax</i> L.	" "
"	<i>Haematopota pluvialis</i> L.	Larva carnivorous. Adult a bloodsucker
"	<i>Helophilus hybridus</i> Lw.	Larva scavenger. Adult on flowers
"	<i>Sericomyia borealis</i> Fall.	" "
"	<i>Tabanus bromius</i> L.	Larva "carnivorous". Adult a "bloodsucker
"	<i>T. sudeticus</i> Z.	" " "
"	<i>Theriopectes distinguendus</i> Verr.	" " "
"	<i>T. tropicus</i> Mg. var. <i>bisignatus</i> Jaenn.	" " "

B. SPHAGNETUM.

Although this has not been much investigated, it is certainly poorly represented at Oxshott. Nearly all the *Sphagnum* was shaded by heavy woods before felling and so was unsuitable, and since the felling animals have been slow in arriving. The only insects that have been noted are the beetle *Cyclo-notum orbiculare* F. and the bug *Microvelia reticulata* Burm. No doubt there is a large microfauna.

C. SUCCESSION ON BARE, WET AREAS.

In the earlier stages of succession there is no distinction in habitat between bare, wet areas and the margins of pools. Gradually, however, mosses form a carpet, which, when dense, becomes the habitat of a different set of animals. The animals characteristic of the early stages of succession still hang on at pool margins, in dried up pools and at damp spots on the paths. In the late summer of 1922 bare, wet areas were very extensive and the animals were those of a pond margin (e.g. *Loricera*, *Bembidium* spp.). In the winter of 1922-3 the ground was much flooded and the *Anchomenus*, *Loricera*, *Notiophilus biguttatus* F. and *Acanthia* were found hibernating under pine bark above the water level. In the summer of 1923 the bare areas were much smaller owing to the spread of *Funaria hygrometrica*; many of the pioneers, however, will tolerate the moss when it is short. The growth of moss is not regular, and does not begin quickly on areas often flooded, so that some bare areas existed in 1925.

In any spot where succession was watched *Bembidium lampros* Hbst. and *Pterostichus diligens* Stm. came in with the mosses and soon became abundant. The latter beetle hibernates in *Polytrichum* and not under pine bark. In 1924 the animals characteristic of bare, damp areas were much scarcer and various new animals appeared. Probably the community eventually changes into one of the normal damp ground series, but this has not yet happened in the places that have been watched. *Polytrichum* at any rate can remain as a local dominant for some years. These facts are summarised in Table XXII. The four stages shown are (1) the bare ground stage, (2) young *Funaria*, (3) *Funaria*, *Ceratodon* and *Polytrichum*, (4) *Polytrichum*. *Ceratodon* may be the main moss where the ground is a little drier, and here the digger wasps *Priocnemis parvulus* Dahlb. (commonly), *Psammochares fuscus* L. (*viaticus*) and *Gorytes quadrifasciatus* F. are found nesting.

The arrival of *Carabus*, the large apterous predaceous beetle, is probably partly correlated with the first abundance of molluscs and earthworms on which it commonly feeds. All these forms are mainly found under bark of pine, etc., in the damp areas, but come out at night. In the following table the correlation between the arrivals is shown:

		1923	1924	1925
Molluscs	<i>Limax maximus</i> L.	A few	A few	Common
	<i>Arion ater</i> L.	"	Common	"
	<i>A. subfuscus</i> Drap.	"	"	"
	<i>Polita alliaria</i> Müll.	—	—	A few
Earthworms		—	A few	Common
Beetle	<i>Carabus catenulatus</i> Sepp.	—	One	"

Table XXII. Succession on bare, wet areas.

1 = Summer 1922. 2 = Summer 1923. 3 = Summer 1924. 4 = Summer 1925

COLEOPTERA					
Beetle	<i>Amara lunicollis</i> Schiödt	Carnivorous	—	2	—
"	<i>Anchomenus 6-punctatus</i> L.	"	1	2	3
"	<i>Bembidium biguttatus</i> F.	"	—	2	—
"	<i>B. bruxellense</i> Wesm.	"	1	—	—
"	<i>B. lampros</i> Hbst.	"	1	2	3
"	<i>B. riparium</i> Ol.	"	1	—	—
"	<i>Carabus catenulatus</i> Scop.	"	—	—	4
"	<i>Cytillus varius</i> F.	?	1	2	—
"	<i>Haltica oleracea</i> L.	Larva on <i>Epilobium</i>	—	—	3
"	<i>Loricera pilicornis</i> F.	Carnivorous	1	—	—
"	<i>Megasternum boletophagum</i> Marsh	Scavenger	—	—	4
"	<i>Notiophilus biguttatus</i> F.	Carnivorous	1	2	3
"	<i>N. palustris</i> Duft.	"	1	—	—
"	<i>Pterostichus angustatus</i> Duft.	"	—	—	3
"	<i>P. diligens</i> Stm.	"	—	2	3
"	<i>P. nigrita</i> F.	"	—	2	—
"	<i>Stenus longitarsis</i> Th.	"	1	—	—
"	<i>S. rogeri</i> Kr.	"	1	—	—
"	<i>Tachyporus chrysomelinus</i> L.	" ?	1	?	3
"	<i>T. hypnorum</i> F.	" ?	1	?	3
HEMIPTERA					
Bug	<i>Acanthia saltatoria</i> L.	Carnivorous ?	1	2	—
"	<i>Nabis rugosus</i> L.	"	—	—	3
"	<i>Trapezonotus arenarius</i> L.	?	1	?	—
COLLEMBOLA					
Springtails	<i>Collembola</i> abundant	Vegetarian	?	?	?
ORTHOPTERA					
Grasshopper	<i>Tettix bipunctatus</i> L.	Vegetarian	1	2	—
CRUSTACEA					
Woodlouse	<i>Porcellio scaber</i> Latr.	Scavenger and ? car- nivorous	—	—	—
ARACHNIDA					
Spider	<i>Erigone atra</i> Bl.	Carnivorous	—	2	—
"	<i>Lycosa amentata</i> Cl.	"	1	—	—
"	<i>Oedothorax fuscus</i> Bl.	"	—	2	—
"	<i>Pirata piraticus</i> Cl.	"	1	—	—
"	<i>Tarentula barpipes</i> Sund.	"	1	—	—
"	<i>Trochosa ruficollis</i> DeG.	"	1	—	—
"	Young of <i>Lycosa</i> , <i>Tibellus</i> , <i>Pirata</i>	"	1	—	—
"	Young of <i>Xysticus</i> sp.	"	1	?	?
ANNELIDA					
Earthworms		Vegetarian	—	—	—
MOLLUSCA					
Slug	<i>Limax maximus</i> L.	Scavenger	—	—	—
Snail	<i>Polita alliaria</i> Müll.	? Carnivorous	—	—	—

D. MOLINIETUM.

Before the fire in 1921 there was an extensive growth of *Molinia* and, since much of it was not destroyed, the animal community connected with it was fully developed when the Common was first visited in 1922; there are thus no observations on the actual changes resulting from the growth of *Molinia* on a given area. The fauna is not unlike that of an ordinary meadow, though there are a number of peculiar forms. Some of the bugs, e.g.

Stenodema and *Trigonotylus* and leafhoppers, e.g. *Tettigonia*, show typical adaptations to grass conditions in their colouring, and, in the case of the bugs, in their elongate shape. Grasshoppers are excessively abundant, and have increased in numbers since 1922. The grass-moths (*Crambus*) were exceedingly abundant in 1922 and to a less extent in 1923. Since then they have been relatively scarce. The same is true of the common rush feeding moth, *Bactra lanceolana* Hb. Perhaps they increased originally as a result of the hot summer in 1921; at any rate no other cause can be suggested. The animals recorded are given in Table XXIII.

The effect of invasion by *Betula* has been discussed in a previous section (p. 257). *Molinia* can grow for a long time in areas which have been invaded by pine. Such *Molinia*, growing in pinewoods, still has associated with it most of the small insects, etc., which normally live under the tufts, e.g. beetles, bugs, spiders and woodlice. The moths and grasshoppers disappear. Many of the fungus beetles of the pinewood hide in the tufts in winter; several weevils, probably attracted from neighbouring leguminous crops, hibernate in *Molinia* growing under the shade of pine. Many of the insects found in the *Calluna* growing in the same situation also occur.

Table XXIII. *Animals of the Molinietum.*

DIPTERA		
Fly	<i>Borborus geniculatus</i> Meq.	Hibernates in tufts. ? Scavenger
"	<i>Loxocera albisetæ</i> Schr.	? ?
"	<i>Sepedon sphegeus</i> F.	Common in autumn
"	<i>Sepsis</i> spp.	Hibernat ^r in tufts. Larva a scavenger
LEPIDOPTERA		
Butterfly	<i>Adopaea sylvanus</i> Esp.	Larva on grasses
"	<i>A. thaumas</i> Hufn.	"
"	<i>Coenonympha pamphilus</i> L.	"
Moth	<i>Crambus hamellus</i> Thnbg.	Larva on grasses. Not common but characteristic
"	<i>C. pascuellus</i> L.	Larva on grasses. Abundant
"	<i>C. tristellus</i> L.	"
Butterfly	<i>Epinephele ianira</i> L.	"
Moth	<i>Euxanthia hamana</i> L.	"
Butterfly	<i>Heodes phloeas</i> L.	Larva on <i>Rumex</i> spp.
Moth	<i>Nomophila noctuella</i> Schiff.	Larva on herbs
Butterfly	<i>Pararge megaera</i> L.	Larva on grasses
Moth	<i>Plusia gamma</i> L.	Larva on herbs
"	<i>Plutella maculipennis</i> Curt.	"
COLEOPTERA		
Beetle	<i>Bradycellus verbasci</i> Duft.	Carnivorous
"	<i>Haltica oleracea</i> L.	Larva on <i>Epilobium</i> . Adult hibernates in tufts
"	<i>Hoplia philanthus</i> Füss.	Larva on plant roots
"	<i>Pterostichus strenuus</i> Pz.	Carnivorous. Adult in tufts in winter
"	<i>Sitones lineatus</i> L.	Leguminosae. Adult in tufts in winter
"	<i>Stenus flavipes</i> Steph.	Carnivorous. Adult in tufts in winter. A characteristic species
"	<i>S. rogeri</i> Kr.	Carnivorous
"	<i>Tachyporus chrysomelinus</i> L.	Carnivorous ? Adult in tufts in winter
"	<i>T. hypnorum</i> F.	" " "

Table XXIII (continued).

HEMIPTERA		
Bug	<i>Nabis major</i> Costa.	Carnivorous
"	<i>N. rugosus</i> L.	"
"	<i>Stenodema calcaratum</i> Fall.	On grasses
"	<i>S. holsatum</i> F.	"
"	<i>Trigonotylus ruficornis</i> Geoff.	"
Leafhopper	<i>Philaenus lineatus</i> L.	"
"	<i>Tettigonia viridis</i> Liv.	"
COLLEMBOLA		
Springtails	<i>Collembola</i> . None identified	Vegetarian and scavengers
ORTHOPTERA		
Grasshopper	<i>Chorthippus elegans</i> Charp.	Herbs
"	<i>C. parallelus</i> Zett.	Herbs. A short winged form not be coming common before 1924
"	<i>Gomphocerus maculatus</i> Thnbg.	Herbs. Abundant. With green forms
"	<i>Metrioptera brachypterus</i> L.	" Abundant
"	<i>Omocestus viridulus</i> L.	"
"	<i>Stauroderus bicolor</i> Charp.	" Commonly with green forms
ARACHNIDA		
Spider	<i>Agelena labyrinthica</i> Cl.	Mainly on bare areas, but catches grass insects, e.g. <i>Philaenus</i>
"	<i>Drassodes troglodytes</i> C.L.K.	Carnivorous
"	<i>Linyphia clathrata</i> Sund.	"
"	<i>Lycosa amentata</i> Cl.	"
"	<i>Pisaura mirabilis</i> Cl.	"
"	<i>Segestria senoculata</i> L.	"
"	<i>Stemonyphantes lineatus</i> L.	"
"	<i>Tibellus oblongus</i> Walek.	"
"	<i>Xysticus erraticus</i> Bl.	"
CRUSTACEA		
Woodlouse	<i>Porcellio scaber</i> Latr.	Scavenger and partly carnivorous
AVES		
Skylark	<i>Alauda arvensis arvensis</i> L.	Mainly seeds
Kestrel	<i>Falco tinnunculus tinnunculus</i> L.	Mainly mice, partly young birds
Partridge	<i>Perdix perdix perdix</i> (L.)	Mainly plants. Partly insects in summer
Pheasant	<i>Phasianus colchicus</i> L.	" " "
Stonechat	<i>Saxicola torquata hibernans</i> Hart.	Mainly insects
MAMMALIA		
Hare	<i>Lepus europaeus occidentalis</i> de Winton	Vegetarian

E. JUNCETUM.

The *Juncus* fauna has not been fully worked out, but probably the number of species is rather low. In individuals, however, the actual rush-feeders are often exceedingly abundant. *Coleophora caespititellu* Zell. must destroy at least half the seeds produced. Some of these rush-feeders also occur on *J. squarrosus*, growing on drier areas, but the fauna given in Table XXV is that connected with *J. effusus*. A few insects are included which visit flowers growing commonly in the Juncetum.

Table XXIV. Animal community in the Juncetum.

HYMENOPTERA		
Bee	<i>Bombus lucorum</i> L.	Female. On <i>Lotus uliginosus</i> and <i>Cirsium</i>
"	<i>Megachile maritima</i> K.	Male. Common on <i>Lotus</i> [<i>palustre</i>]
"	<i>M. willughbiella</i> K.	"
"	<i>Psen unicolor</i> V. de Lind.	Female hunting " leafhoppers amongst
"	<i>Psammochares? piliiventris</i> Mor. (cardui)	Female on <i>Lotus</i> [<i>Juncus</i>]
Wasp	<i>Vespa germanica</i> Fab.	Worker (probably fly-hunting) in <i>Juncus</i>
"	<i>V. vulgaris</i> L.	" " "
"	<i>V. rufa</i> L.	" " "

Table XXIV (continued).

DIPTERA		
Fly	<i>Dolichopus pennatus</i> Mg.	Predaceous
"	<i>Gymnopternus nanus</i> Meq.	"
"	<i>Tachydromia flavipes</i> F.?	"
"	<i>Psectrosciara coxendix</i> Verr.	Adults, sometimes very common on heads of <i>Juncus</i> . Larva ? scavenger
LEPIDOPTERA		
Butterfly	<i>Adopaea silvanus</i> Esp.	On flowers of <i>Lotus</i>
Moth	<i>Bactra lanceolana</i> Hb.	Larva on <i>Juncus</i> . Abundant 1922-3
"	<i>Coleophora caespititiella</i> Zell.	" " Abundant
"	<i>C. glaucicolella</i> Wood	" " "
"	<i>Gliphipteryx thrasonella</i> Scop.	" " Common 1924-5
COLEOPTERA		
Beetle	<i>Crepidodera transversa</i> Marsh	Vegetarian. Abundant in 1924
"	<i>Cyphon variabilis</i> Thnbg.	Larva carnivorous
"	<i>Pterostichus strenus</i> Pz.	Carnivorous
"	<i>Rhagonycha fulva</i> Scop.	Carnivorous (sometimes on flowers of <i>Lotus</i>)
"	<i>Xantholinus linearis</i> Ol.	? Carnivorous
HEMIPTERA		
Bug	<i>Anthocoris nemorum</i> L.	Carnivorous
"	<i>Trigonotylus ruficornis</i> Geoff.	Vegetarian
Leafhopper	<i>Athysanus sordidus</i> Zett.	"
"	<i>Conomelus limbatus</i> Fab.	" Abundant
"	<i>Limotettix antennata</i> Boh.	"
ARACHNIDA		
Spider	<i>Chromolothus festivus</i> C.L.K.	Carnivorous. Web on heads of <i>Juncus</i>
"	<i>Dietynna luteus</i> F.	" " "
"	<i>Pisaura mirabilis</i> Cl.	Carnivorous

F. SPECIAL PLANTS.

Certain plants characteristic of wet areas always have certain animals, either vegetarians or flower visitors, associated with them. These animals certainly seek the plant rather than any special conditions and so are given separately rather than in the community in which the plant grows. Thus the flowers of *Potentilla erecta* are always visited abundantly by the fly *Hercostomus nigripennis* Fall; and the bees *Prosopis brevicornis* Nyl. and *P. genalis* Thoms., occasionally by workers of *Bombus agrorum* Fab.

Rumex acetosella is the food of the beetles *Cryptocephalus fulvus* Goeze, *Apion rubens* Steph. and *Rhinoncus castor* F. These are found with the plant wherever it occurs.

Ragwort (*Senecio jacobaea*) and other species of *Senecio* are fed on by the beetle *Longitarsus jacobaeae* Wat., and the flowers of this and other Yellow Composites are visited by the fly *Sicus ferrugineus* L. and bees of the genus *Halictus*.

The species connected with *Salix* (broad-leaved species), with *Ulex europaeus* and with *Rubus* are so numerous that they are given in Tables XXV, XXVI, and XXVII. The flowers of the first two plants are important as being the main source of food for the spring bees, and of various other hibernated insects.

Table XXV. *Animals connected with Salix spp.*

M. = Male. F. = Female. W. = Worker

HYMENOPTERA			
Wasp	<i>Ancistrocerus callosus</i> Thoms.	On flowers	F.
Bee	<i>Andrena albicans</i> Müll.	"	M. F.
"	<i>A. bimaculata</i> K.	"	M.
"	<i>A. clarkella</i> K.	"	M. F.
"	<i>A. dorsata</i> K.	"	M. F.
"	<i>A. fulva</i> Schrk.	"	F.
"	<i>A. gwynana</i> K.	"	M.
"	<i>A. parvula</i> K.	"	F.
Hive bee	<i>Apis mellifera</i> L.	"	W.
Humble bee	<i>Bombus agrorum</i> F.	"	F.
"	<i>B. jonellus</i> K.	"	F.
"	<i>B. lapidarius</i> L.	"	F.
"	<i>B. lucorum</i> L.	"	F.
"	<i>B. pratorum</i> L.	"	F.
"	<i>B. terrestris</i> L.	"	F.
Bee	<i>Halictus minutus</i> Zett.	"	F.
"	<i>H. punctatissimus</i> Sch.	"	F.
Digger wasp	<i>Psammochares fuscus</i> L. (<i>vineticus</i>)	"	F.
DIPTERA			
Fly	<i>Chilosia vulpina</i> Mg.	"	M.
"	<i>Chortophila muscaria</i> Mg.	"	M. F.
"	<i>Eristalis intricarius</i> L.	"	M.
"	<i>Orthoneura geniculata</i> Mg.	"	M.
"	<i>Platychirus albimanus</i> F.	"	M. F.
"	<i>Rhabdophaga saliciperda</i> Duf.	Galls on the stems with two Chalcid parasites	
"	<i>Scatophaga stercoraria</i> L.	On the flowers	M.
"	<i>Syrphus lasiophthalmus</i> Zett.	"	M. F.
LEPIDOPTERA			
Moth	<i>Cerura furcula</i> L.	Larva on leaves	
Butterfly	<i>Vanessa io</i> L.	On the flowers	
COLEOPTERA			
Beetle	<i>Adalia bipunctata</i> L.	On the flowers	
"	<i>Crepidodera aurata</i> Marsh	Feeds on the leaves	
"	<i>Melanophthalma gibbosa</i> Hbst.	On the flowers	
"	<i>Meligethes ovatus</i> Stm.	"	
HEMIPTERA			
Bug	<i>Anthocoris nemoralis</i> F.	On the flowers	
"	<i>A. nemorum</i> L.	"	
Psyllid	<i>Psylla salicicola</i> Först.	Feeds on the leaves	

Table XXVI. *Animals associated with Ulex.*

M. = Male. F. = Female. W. = Worker

HYMENOPTERA			
Sawfly	<i>Abia lonicerae</i> L.	On the flowers	F.
Bee	<i>Andrena bimaculata</i> K.	"	M.
"	<i>A. dorsata</i> K.	"	M.
"	<i>A. gwynana</i> K.	"	M.
Hive bee	<i>Apis mellifera</i> L.	"	W. abundant
Humble bee	<i>Bombus agrorum</i> Fab.	"	F. common
"	<i>B. ruderarius</i> Müll. (<i>derhamellus</i>)	"	F.
Bee	<i>Halictus flavipes</i> F.	"	F.
"	<i>H. punctatissimus</i> Sch.	"	F.
DIPTERA			
Fly	<i>Eristalis pertinax</i> Scop.	"	M. F.
"	<i>Euaresta conjuncta</i> Lw.	Adult hibernates in <i>Ulex</i>	
"	<i>Platychirus albimanus</i> F.	On the flowers	M. F.
"	<i>P. scutatus</i> Mg.	"	M.

Table XXVI (*continued*).

DIPTERA		
Fly	<i>Scatophaga stercoraria</i> L.	On the flowers M.
"	<i>Syrphus auricollis</i> Ztt.	"
"	<i>S. cinctellus</i> Zett.	"
"	<i>S. lasiophthalmus</i> Ztt.	"
"	<i>S. punctulatus</i> Verr.	"
"	<i>S. torvus</i> O.S.	"
"	<i>Tephritis vespertina</i> Lw.	Adult hibernates in gorse
LEPIDOPTERA		
Moth	<i>Laspeyresia ulicetana</i> Hw.	Larva on gorse
"	<i>Scythris grandipennis</i> Hw.	"
COLEOPTERA		
Beetle	<i>Adalia bipunctata</i> L.	On the flowers
"	<i>Apion ulicis</i> Först.	Larva on the seeds
"	<i>Micrambe vini</i> Pz.	Larva on the flowers
"	<i>Sitones regensteiniensis</i> Hbst.	Larva on <i>Ulex</i>
"	<i>S. tibialis</i> Hbst.	"
HEMIPTERA		
Bug	<i>Asciodema obsoletum</i> Fieb.	On <i>Ulex</i>
"	<i>Dictyonota strichnocera</i> Fieb.	"
ARACHNIDA		
Spider	<i>Epeira cornuta</i> Cl.	Webs of the young abundant on <i>Ulex</i> in the spring

Table XXVII. *Insect visitors of flowers of Rubus fruticosus (agg.)*.

M. = Male. F. = Female. W. = Worker

HYMENOPTERA		
Bee	<i>Apis mellifera</i> L.	W. abundant
"	<i>Bombus agrorum</i> Fab.	F. W. common
"	<i>B. hortorum</i> L.	M. W.
"	<i>B. lucorum</i> L.	M. F. W. common
"	<i>B. pratorum</i> L.	M. common. W. only where a scrub has developed
"	<i>B. ruderarius</i> Müll. (<i>derhamellus</i>)	M. F.
"	<i>B. terrestris</i> L.	M. F. W.
Digger wasp	<i>Cercoris labiata</i> F.	M. Cf. Table I
"	<i>C. rybyensis</i> L.	M. "
Bee	<i>Chelostoma campanularum</i> K.	M.
"	<i>Coelioxys elongata</i> Lep.	M. F. Parasite of <i>Megachile</i>
Digger wasp	<i>Gorytes quadrifasciatus</i> F.	M.
Bee	<i>Halictus flavipes</i> F.	F. Cf. Table I
"	<i>H. nitidiusculus</i> K.	F.
Ruby wasp	<i>Hedychridium minutum</i> Lep.	Cf. Table I
Bee	<i>Megachile circumcincta</i> Lep.	F.
"	<i>M. maritima</i> K.	M. Cf. Table I
"	<i>M. versicolor</i> Smith	M.
"	<i>M. willughbiella</i> K.	F. Cf. Table XXIX
Digger wasp	<i>Nysson interruptus</i> F.	M. Cf. Table I
Wasp	<i>Odynerus pictus</i> Curt.	F.
Bee	<i>Osmia leucomelaena</i> K.	F.
Digger wasp	<i>Oxybelus uniglumis</i> L.	M. F. Cf. Table I
Bee	<i>Prosopis brevicornis</i> Nyl.	M. F.
"	<i>P. communis</i> Nyl.	M. F.
"	<i>P. confusa</i> Nyl.	M. F. common
"	<i>P. genalis</i> Thoms.	M. F. Cf. Table XXIX
Digger wasp	<i>Psen shuckardi</i> Wesm.	M. Cf. Table I
Bee	<i>Psithyrus barbutellus</i> K.	M. parasite of <i>Bombus hortorum</i>
"	<i>Ps. distinctus</i> Perez.	M. parasite of <i>B. lucorum</i>
"	<i>Ps. quadricolor</i> Lep.	M. common parasite of <i>B. pratorum</i>
"	<i>Saropoda bimaculata</i> Pz.	M. F. common. Cf. Table I
Digger wasp	<i>Sphex campestris</i> Latr.	M. "
"	<i>S. sabulosa</i> L.	M. common. F. Cf. Table I
"	<i>Tachysphex unicolor</i> Pz.	M. Cf. Table I

Table XXVII (continued).

DIPTERA		
Fly	<i>Chilosia scutellata</i> Fall.	Larva ? fungi
"	<i>Empis aestiva</i> Lw.	Carnivorous
"	<i>Eristalis arbustorum</i> L.	Cf. Table XXII
"	<i>E. intricarius</i> L.	"
"	<i>Fabriceiella ferox</i> Pz.	Larva parasite of large caterpillars
"	<i>Sicus ferrugineus</i> L.	
"	<i>Volucella pellucens</i> L.	Commensal of wasps
"	<i>V. plumata</i> L.	Commensal of <i>Bombus</i>
LEPIDOPTERA		
Butterfly	<i>Adopaca sylvanus</i> Esp.	Cf. Table VII
"	<i>Epinephele janira</i> L.	
COLEOPTERA		
Beetle	<i>Byturus tomentosus</i> F.	Cf. Table VII
"	<i>Rhagonycha fulva</i> Scop.	
"	<i>Strangalia armata</i> Hbst.	Cf. Table VII
HEMIPTERA		
Bug	<i>Anthocoris nemorum</i> L.	
"	<i>Plagiognathus arbustorum</i> F.	Cf. Table VII

G. PINE STUMPS AND FUNGI.

The pine stumps and the fungi connected with them form a relatively clear-cut habitat, occurring in every part of the area. Fungi are by no means all equally attractive to insects, and, though this has not been worked out in detail, it is mainly the species connected with the stumps that have a large fauna. The community is probably nearly the same as that which is associated with fungi in the pinewood. The animals at the base of the food chain are larvae of small flies and Collembola. The staphylinid beetles feed on these but there are no details of their feeding habits.

The pine stumps are the home of another set of animals which gradually destroy the stumps. There is probably a good deal of difference between the early stages of colonisation of fresh pine stumps and of those which have been burnt. This has not been much studied at Oxshott, but in a general way the effect of burning is to cut out the early stages of the succession. A number of animals, often highly specialised to life under bark, only occur under fresh stumps, or those not badly burnt. The beetle *Melanophila acuminata* DeG. which is peculiar to burnt pine stumps and usually arrives while the fire is still smoking, has not been seen at Oxshott, though recorded from other heaths in southern England.

The normal course of succession probably begins with arrival of Scolytid beetles (e.g. *Hylastes*). With them come their special enemies, such as the beetles belonging to the genus *Rhizophagus*, which feed on the Scolytids. In the solid wood *Asemum* and *Criocephalus* make their burrows. The holes formed allow fungi to enter and their mycelia soon become abundant under the bark and in the wood. With them come abundant Collembola and their enemies the staphylinid beetles, small carabids; probably the flat, bark-haunting bugs also feed on them. Quite soon queen ants arrive and make their nests under the bark, and later the workers begin to excavate their

galleries in every direction. These activities soon loosen the bark and a kind of humus collects beneath it. As soon as ants have become abundant the woodpeckers attack the stumps and are perhaps one of the most important agencies in their destruction. When the bark has become really loose the specialised bark animals disappear and their place is taken by an assemblage of forms that need a dark, damp habitat. Such are woodlice, molluscs, earthworms and the carabid beetles which prey on them. Probably at Oxshott a stump may disappear in about eight years but the length of time would vary very considerably with local conditions. Under the shelter of a pine wood the stumps might persist almost indefinitely, while in damp, exposed situations the decay is rapid.

The stumps are often an important addition to the habitat in which they are situated because they may be used by whatever animals occur as hibernation quarters (beetles, wasps, flies), nesting sites (digger wasps, ants, spiders) or as shelter by day in dry areas (molluscs, beetles). The existence of stumps probably allows various animals to maintain themselves in such a habitat as a Callunetum, animals which would normally have to wait for more mesophytic conditions to be established.

Sclerodermae have a little fauna of their own. They grow mainly in the birch-scrub stages and often contain the beetles *Atheta xanthoptera* Steph., *Cryptophagus lycoperdi* Hbst. and *C. punctipennis* Bris. Perhaps the first named feeds on the larvae of the Cryptophagi.

Table XXVIII. *Animals associated with fungi.*

DIPTERA		
Fly	<i>Chilosia longula</i> Ztt.	Larva in <i>Boletus bovinus</i>
"	<i>Forcipomyia</i> spp.	Can be bred abundantly from fungi
"	<i>Leria cineraria</i> Lw.	Larva on fungus (<i>Sparassis crespae</i>)
"	<i>Limosina antennata</i> Duda	" ? (<i>Sparassis crespae</i>)
"	<i>L. luteilabris</i> Rdt.?	" " "
"	<i>L. parapsio</i> Dahl.	" " "
"	<i>Mycetophilids</i> common	Larva on fungus
COLEOPTERA		
Beetle	<i>Aleochara brunneipennis</i> Kr.	Carnivorous (<i>Lactorius turpis</i>)
"	<i>Atheta xanthoptera</i> Steph.	" "
"	<i>Autalia impressa</i> Ol.	(<i>L. turpis</i>)
"	<i>Boletobius pygmaeus</i> F.	Carnivorous
"	<i>B. trinotatus</i> Er.	" (<i>L. turpis</i>)
"	<i>Gyrophana gentilis</i> Er.	" "
"	<i>Philonthus marginatus</i> F.	" (<i>L. turpis</i>)
"	<i>Ph. proximus</i> Kr.	" "
"	<i>Ph. varians</i> Pk.	" "
"	<i>Proteinus brachypterus</i> F.	" "
"	<i>P. ovalis</i> Steph.	" (<i>L. turpis</i>)
"	<i>Quedius cinctus</i> Pk.	" "
"	<i>Tachinus laticollis</i> Gr.	" "
ANNELIDA		
Earthworm		Vegetarian (<i>Polyporus schweinitzi</i>)
MOLLUSCA		
Slug	<i>Arion ater</i> L.	Vegetarian eating <i>Boletus bovinus</i>

Table XXIX. *Animals associated with pine stumps.*

HYMENOPTERA		
Ant	<i>Acanthomyops niger</i> L.	Nesting
"	<i>Formica fusca</i> L.	"
"	<i>Leptothorax acervorum</i> F.	" (early stages)
Bee	<i>Megachile willughbiella</i> K.	Probably nests in the very rotten wood
Ant	<i>Myrmica</i> spp.	Nesting
Bee	<i>Prosopis genalis</i> Thoms.	Probably nests in the very rotten wood
Digger wasp	<i>Psen unicolor</i> V. de Lind.	" "
Wasp	<i>Vespa germanica</i> F.	Females hibernating
"	<i>V. vulgaris</i> L.	"
DIPTERA		
Fly	<i>Exechia spinigera</i> Winn.?	Larva on fungi
"	<i>Mycetophilus ocellus</i> Walk.	Larva on fungi (adults sometimes hide under bark)
"	<i>Phaonia</i> spp. and other muscids	Hibernating
"	<i>Tachypeza nubila</i> Mg.	Larva carnivorous in rotten wood. Adult on small flies
LEPIDOPTERA		
Moth	<i>Oecophora sulphurella</i> F.	Larva on rotten wood. Pupa under bark
COLEOPTERA		
Beetle	<i>Adalia bipunctata</i> L.	Hibernating
"	<i>Agathidium laevigatum</i> Er.	Fungus
"	<i>Anisotoma humeralis</i> Kug.	"
"	<i>Asemum striatum</i> L.	Larva in solid wood
"	<i>Atheta aequata</i> Er.	Carnivorous
"	<i>A. linearis</i> Gr.	" early stages of stumps
"	<i>Baptolinus alternans</i> Gr.	"
"	<i>Bradycellus harpalinus</i> Dj.	Sheltering
"	<i>Cerylon histeroideus</i> F.	Larva carnivorous
"	<i>Coccidula</i> spp.	Hibernating
"	<i>Conosoma pubescens</i> Gr.	Carnivorous (later stages)
"	<i>Crioccephalus fesus</i> Kr.	Larva in solid wood (early)
"	<i>Ditoma crenata</i> F.	Larva under bark, carnivorous (early)
"	<i>Dromius angustus</i> Brulle	Carnivorous (early)
"	<i>Elater balteatus</i> L.	Larva on rotten wood
"	<i>Helops striatus</i> Fourc.	Probably mainly sheltering
"	<i>Homalium rivulare</i> Pk.	Carnivorous. Mainly in fungi
"	<i>Hylastes ater</i> Pk.	Larva in wood and bark (early stages)
"	<i>H. cunicularius</i> Pk.	" " "
"	<i>H. palliatus</i> Gyll.	" " "
"	<i>Leistus spinibarbis</i> F.	Carnivorous (later stages)
"	<i>Leptusa fumida</i> Er.	" (early stages)
"	<i>Melanotus rufipes</i> Hbst.	Larva on wood (early stages)
"	<i>Mycetoporus lucidus</i> Er.	Carnivorous (fungi)
"	<i>Nebria brevicollis</i> F.	" (later stages)
"	<i>Ocypus morio</i> Gr.	"
"	<i>Pentarthrum huttoni</i> Woll.	Larva on wood
"	<i>Phloeconomus punctipennis</i> Th.	Carnivorous (early stages)
"	<i>Phloeopora reptans</i> Gr.	" "
"	<i>Phyllodrepa vilis</i> Heer.	" "
"	<i>Pissodes notatus</i> F.	Larva on wood
"	<i>Pterostichus angustatus</i> Duft.	Carnivorous. Burnt stumps
"	<i>P. vulgaris</i> L.	"
"	<i>Quedius maurus</i> Sahlb. (<i>fageti</i>)	"
"	<i>Rhizophagus bipustulatus</i> F.	" (early stages)
"	<i>R. ferrugineus</i> Pk.	" "
"	<i>Scaphisoma agaricinum</i> L.	Fungi
"	<i>Silpha atrata</i> L.	Carnivorous? (later stages)
"	<i>Sphindus dubius</i> Gyll.	Fungi (early stages)
"	<i>Thanasimus formicarius</i> L.	Carnivorous, esp. on dead trees
"	<i>Xantholinus linearis</i> Ol.	"
HEMIPTERA		
Bug	<i>Piezostethus cursitans</i> Fall.	" (early stages)

Table XXIX (*continued*).

NEUROPTERA		
Snakefly	Rhaphidia maculicollis Steph.	Larva carnivorous (early stages)
COLLEMBOLA		
Springtails	Collembola abundant	Vegetarian
	Campodea sp.	"
ARACHNIDA		
Spider	Agelena labyrinthica Cl.	Hibernating and making webs on the stumps when there are no bushes
"	Prosthesima petiverii Scop.	Hiding egg cocoons
"	Trochosa ruricola DeG.	" and hibernating
"	Salticus scenicus Cl.	Hunts on the stumps (catches <i>Oecophora</i>)
CRUSTACEA		
Woodlouse	Porcellio dilatatus Brandt	Scavenger and partly predaceous (later stages)
"	P. scaber Latr.	Scavenger and partly predaceous (later stages)
CHILOGNATHIA		
Centipedes	Lithobius spp. and others	Carnivorous. Common in later stages
MOLLUSCA		
Slug	Arion ater L.	Vegetarian. Common in later stages
"	A. subfuscus Drap.	" " "
"	Limax maximus L.	" " "
ANNELIDA		
Earthworms		Vegetarian. Common in later stages
AVES		
Great Spotted Woodpecker	Dryobates major anglicus Hart.	Feeds on ants and other insects
Green Woodpecker	Picus viridis virescens Brehm.	" " "
MAMMALIA		
Rabbit	Oryctolagus cuniculus L.	Use the stumps as special depositories for dung

CONCLUSION

The animals found on the felled and burnt areas at Oxshott Common in the years 1922-5 have been recorded and some of their effects on one another, and of their relations to plant succession, have been described. It would be premature to make any generalisations about heath-animals.

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YEW COMMUNITIES OF THE SOUTH DOWNS

By A. S. WATT.

(With Plates IV and V, Folding Table, and seven Figures in the Text.)

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This paper records an enquiry into the origin, structure, development and fate of some yew communities of the South Downs (Hants and Sussex); their relation to scrub, ash oakwoods and beechwoods is discussed and evidence brought forward to show that these yew-woods are migratory societies of scrub.

The yew (*Taxus baccata*) is widespread on the chalk hills of West Sussex and East Hampshire, growing isolated in scrub, in ash-oakwoods and beech-woods, and in larger or smaller groups with or without other trees. In many cases at least the apparently fortuitous distribution of scattered yews can be explained in accordance with the findings of this study: it is, however, with the yew in the larger groupings that the paper mainly deals.

TOPOGRAPHY

The yew communities examined lie in the neighbourhoods of Butser Hill and Ditcham Park and of Goodwood, the former, an area familiar to students of chalk vegetation through the work of Tansley¹ and Adamson¹—the latter the scene of the author's work on the Sussex beechwoods². The following yew-woods have been examined. Opposite the name of each the aspect and locality are given:

1. Bottom "A," valley facing S. Southern slope of Butser Hill.
2. Bottom "B," valley facing S.E. and S.S.E. Southern slope of Butser Hill.
3. Kingley Vale, valley facing S. 4 miles N.W. of Chichester (Goodwood area).
4. Hillhampton Bottom, valley facing S.S.E. Southern slope of Butser Hill.
5. Wascombe Bottom, valley facing S.E. Southern slope of Butser Hill.
6. Chilgrove Hill, slope facing N.E. 2½ miles N.W. of West Dean (Goodwood area).
7. Downley Brow, slope facing N.W. 1 mile N.E. of Ditcham House.
8. Holt Down, slope facing N.W. 1 mile S.W. of Butser Hill.
9. Deep Combe, valley facing S.S.W. 1½ miles N.E. of East Dean (Goodwood area).
10. Stead Combe, valley facing E. 1 mile W. of Cocking (Goodwood area).

A brief consideration of the geographical position of these yew-woods in relation to the large forest area of West Sussex and East Hampshire will be of value in helping to assign to the yew-woods their proper place in the context of South Down vegetation. Quite detached from the main body of woodland and set in a background of grassland are, to the south, Kingley Vale, and to the west, Bottoms "A" and "B," Hillhampton and Wascombe Bottoms and Holt Down. Deep Combe, Chilgrove Hill and Downley Brow are just on the outskirts of progressive woodland and may be continuous with the main body. Stead Combe in the Cocking Gap lies near the north escarpment in a region with much chalk grassland clothing the gentler slopes of the Gap and with progressive woodland in the neighbourhood. On the whole, therefore, the yew-woods studied grow on the outskirts of, or are quite detached from, the main forest area.

¹ **Adamson**. "The Woodlands of Ditcham Park, Hampshire." This JOURNAL, **9**, 1922, pp. 114-219. **Tansley**. "Early Stages of Redevelopment of Woody Vegetation on Chalk Grassland." This JOURNAL, **10**, 1923, pp. 168-177. **Tansley** and **Adamson**. "The Chalk Grasslands of the Hampshire-Sussex Border." This JOURNAL, **13**, 1925, pp. 177-223.

² **Watt**. "On the Ecology of British Beechwoods with special reference to their regeneration." This JOURNAL, **11**, 1923, pp. 1-48; **12**, 1924, pp. 145-204; **13**, 1925, pp. 27-73.

SOME FACTORS AFFECTING THE DEVELOPMENT OF YEW COMMUNITIES

Soil.

The soil in all the yew communities is calcareous except in the yew society above Deep Combe where the overlying friable loam is about 14 in. deep. In different parts of the valleys the soil varies from 6 in. on exposed steep slopes to 18 in. on gentler and sheltered slopes. In the valley bottoms the depth has not been determined but is no doubt much greater. No marked effect of soil in influencing the development of yew communities has been observed in the areas studied.

Wind.

All the yew-woods described, except Nos. 6-8, occupy valleys opening southwards to eastwards. Different parts of them are thus in varying degree exposed to the prevailing south-west winds, the most sheltered part varying with the lie of the valley but being generally near the valley head. That wind is a significant factor in yew-wood distribution and development is inferred from the prevalence of wind trimming among the shrubs in the near neighbourhood, from the general limitation of the yew-woods to the valleys, and from their greater and more rapid extension along sheltered slopes and to leeward of existing communities. Further, the general statement may be made here that woody vegetation first colonises the most sheltered parts of the valleys, extending thereafter to less sheltered parts.

In the three yew-woods growing on slopes the most rapid development takes place to leeward along the slope.

Rabbits.

The recent studies of Tansley and of Tansley and Adamson demonstrate the far-reaching effect on vegetation of heavy rabbit grazing. Severe grazing causes grassland degeneration and exposure of the soil, which may then be colonised by herbaceous and woody species avoided by rabbits. Even the spiny hawthorn and blackthorn are severely attacked, but the fact of greatest significance for the present study is the susceptibility of the yew. Like ash, oak and beech it requires the assistance of scrub for successful colonisation of grassland; and the efficiency of scrub for this purpose will depend upon the measure of immunity enjoyed by the scrub constituents. Of these juniper is most shunned by rabbits, and this property combined with that of wind resistance¹ gives to the juniper a significance in yew-wood establishment not possessed by any other shrub. Much importance is therefore attached to the distribution of juniper which is absent from some valleys and scarce or abundant in different parts of others—this variation in frequency influencing the structure and development of the succeeding vegetation. Adequate attention has not yet been paid to the factors governing juniper distribution but the impression is gained that juniper flourishes best on relatively shallow soils, often exposed to the prevailing winds.

¹ Watt. *L.c.* 1924, p. 159.

GENERAL DESCRIPTION OF THE VEGETATION

The phenomena described in this paper can be explained as the result of the natural processes of invasion and succession.

The difficulties confronting yew ecesis prevent effective yew colonisation of grassland. Yew, however, can invade scrub, where conditions favour its spread, and the original scrub is then ultimately suppressed. Thus yew-wood is reached through a series of intermediate stages, with or without ash, in which longevity and tolerance of shade are the chief factors in the equipment of the yew enabling it to compete successfully with its associates. Upon the death of old yews rabbit activity often prevents the regeneration of the gaps formed: hence the wood degenerates and ultimately abandons the area. Inasmuch as colonisation by scrub usually begins near the head of the valley, so this part is the first to be abandoned by the degenerating yew-wood.

In this succession from scrub to yew-wood two seres are recognised, called respectively the *juniper sere* and the *hawthorn sere* after the shrubs dominant in the initial scrub. In the hawthorn sere there are two varieties, one with ash, the other without. Briefly summarised the successions are as follows, all three sometimes contributing to the "make up" of a valley yew-wood.

Juniper sere. Scrub (juniper)→Yew scrub→Developing Yew-wood→Yew-wood.
Hawthorn sere. Scrub (hawthorn)→Yew scrub→Developing Yew-wood→Yew-wood.
 (without ash)
Hawthorn sere. Scrub (hawthorn) $\xrightarrow{\nearrow \text{Ash scrub} \searrow}$ Yew-ash scrub→Yew-ashwood→Yew-wood.
 (with ash) $\xrightarrow{\searrow \text{Yew scrub} \nearrow}$

The juniper sere is met with on the more exposed places and, once yew invasion starts, is characterised by a relatively quick transition to pure yew-wood. The hawthorn sere begins with a scrub less efficient to protect yew and the intermediate stages are long drawn out; pure yew-wood appears late. In the succession with ash, this tree may appear before, along with, or after, effective yew invasion of scrub. This sere occurs in the sheltered parts of valleys or on the lee side of woodland. The variety without ash is found in both sheltered and partly exposed localities.

In Section I, attention is mainly directed to a study of the structure, development and fate of the yew-wood, whilst the relation of this community to other woody communities—ash-oakwood and beechwood—forms the subject-matter of Section II.

SECTION I. STRUCTURE, DEVELOPMENT AND FATE OF THE YEW-WOODS

(a) THE JUNIPER SERE.

The different stages of the juniper sere mostly occupy, but are not strictly confined to, exposed places (Pl. IV, Phot. 1, and Figs. 1 and 2, pp. 286–7).

Of the 22 species recorded from this sere, juniper and yew are clearly the

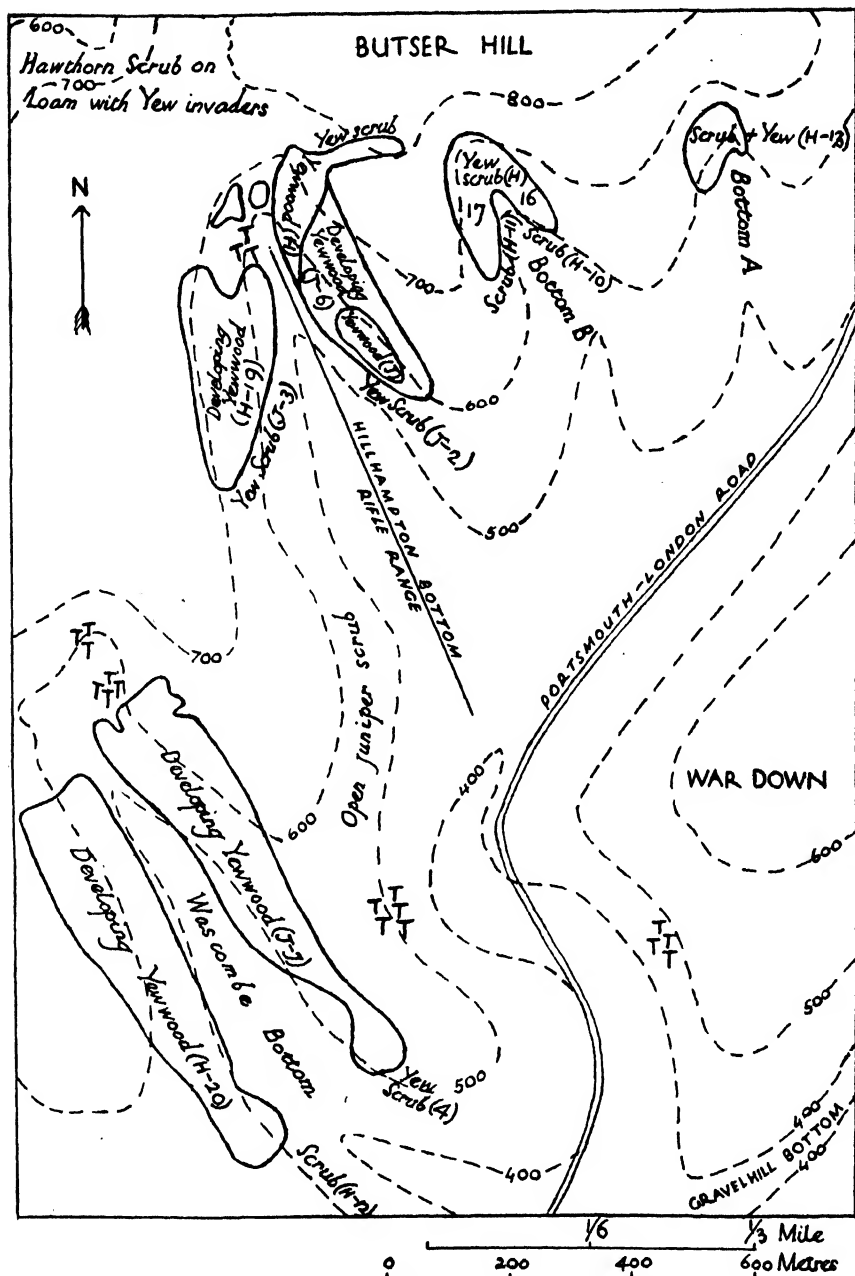


FIG. 1. Sketch-map of area south of Butser Hill showing yew-woods in the valleys. Groups of yews not in the valleys are marked TT. The woods have originated near the heads of the valleys and are moving outwards along the slopes. In Hillhampton Bottom the area first colonised is being abandoned; three old yews marked T are relicts. The whole of the head of Wascombe Bottom has been abandoned and is being recolonised by yews marked T.

main constituents: the rest are quite subordinate (list of species facing p. 304, columns 1-8)¹.

The general course of development is as follows. The juniper scrub, which at Kingley Vale consists of scattered or locally dense individuals about 3 ft.

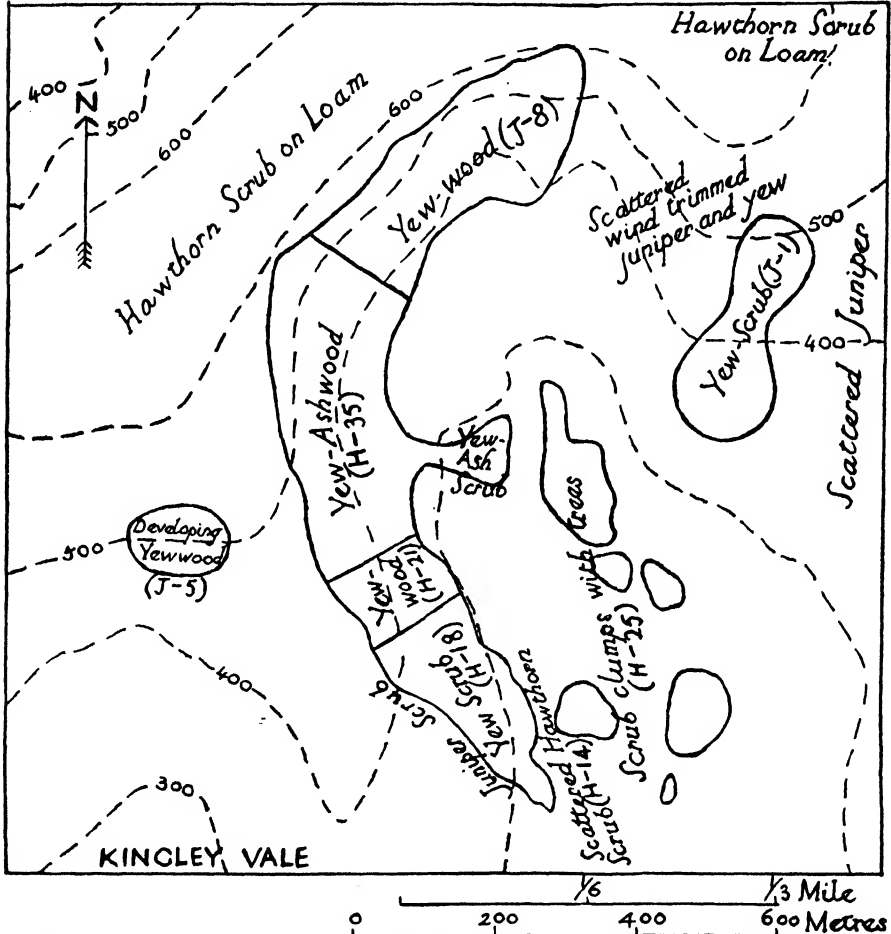


FIG. 2. Sketch-map of Kingley Vale showing development of yew-wood mainly on the slope sheltered from the prevailing south-west winds. The juniper sere (*J*)¹ occupies the more exposed parts, the hawthorn sere (*H*)¹ without ash, areas of mean exposure, and the hawthorn sere with ash the most sheltered part of the valley.

high and lopsided, is invaded by yew. Where the juniper forms the nucleus of a closed scrub yew invasion may be general, as for example on the eastern spur of Kingley Vale (Fig. 2, 1)¹ where yews from a few inches to 10 ft. are found but the majority are from 4 to 5 ft. In open juniper scrub yew invasion

¹ The reference number of the list of species (facing p. 304) corresponds with the number of the locality, given in the figures, from which the list was made. Thus *J*-8 means juniper sere, list 8.

is more sporadic and results in the formation of clumps consisting of yew families girt by scrub. A family consists of a central older yew with a richly branched and spreading crown (pioneer form) near which grow younger yews whose cleaner stems and lopsided crowns are due to the shading effect of the pioneer. In the scrub round the clumps small yews are growing up. This grouping of younger, straighter yews round aged pioneers is obvious in the yew scrub and developing yew-wood and can usually be made out in the pure yew-wood.

The older pioneer yew invaders show the effects of the prevailing wind but the younger yews growing up with them have mostly erect leading shoots. The sheltering effect of the yew is also seen in the improved growth of shrubs already present, e.g. juniper in the lee of a clump or in the presence of others may attain to 10 ft., a height not commonly found isolated in exposed situations. This stage in the development of yew-wood, when yew has clearly become established and is spreading, is called *yew scrub*. The most important associated species are *Cornus*, *Prunus spinosa*, *Rubus fruticosus* (agg.), *Crataegus*, *Ilex* and *Sambucus*.

The next stage, when the balance of dominance is with the yew, is called the *developing yew-wood*, which arises merely as a result of the continued increase in size of the individual yews, the enlargement of yew families and the establishment of fresh ones in the scrub between them. That this has taken place is proved by the dead remains of abundant juniper and of some hawthorn, bramble and *Clematis* found under the yews. As a result partly of the increased shelter afforded to the shrubs by the taller yews and partly by their lateral shading effect, the shrubs attain a much greater height. For example, in the developing yew-wood of the eastern slopes of Hillhampton and Wascombe Bottoms (Fig. 1, 6 and 7) the juniper has a columnar form and sometimes reaches 18-20 ft. in height. The number of species is the same as in the yew scrub and although the growth of the shrubs has improved, there is on the whole no increase in their frequency, this being prevented by the spread of the yews.

The continued growth and spread of the yew finally result in *pure yew-wood* by the suppression of the accompanying shrubs, the dead remains of these, particularly of juniper, being found on the floor. Suppression is complete on the eastern slope of Hillhampton Bottom where the yew-wood is pure, but at the head of Kingley Vale (Fig. 2, 8) occasional *Ilex* and rare straggling *Crataegus* and *Prunus spinosa* still find a place in the canopy, above which rare ash and occasional whitebeam (*Sorbus aria*) raise their crowns. The dominance of the yew is complete to a degree found in no other British tree community: the shrub layer and ground flora are absent and mosses are rare.

In this sere the yew attains a height of about 30 ft. (9 m.), with a circumference of 7 ft. 1 in. (2.12 m.) (= average of six large yews, the largest measuring

9 ft. 11 in. or 3 m.). Since the stages of the succession are completed within the life history of the yew, the size of the yews in different parts of the yew-wood may be used as evidence of the direction of spread. Applying this to the yew-wood at the head of Kingley Vale we find that the yew has invaded from the north-west corner outwards along the slope as well as up and down, but fastest along the slope and faster up than down. In this locality further movement along the slope is apparently held up, but additions to the upper and lower margins of the wood are being made from yew scrub.

The habitat is unfavourable for the establishment and growth of ash and oak, both of which are rare to occasional and mostly of poor growth; ash trees established near the bottom of the valleys show better growth but even there some suffer from wind. *Sorbus aria*, however, grows quite well and is a frequent constituent of the developing yew-woods on the eastern slopes of Hillhampton and Wascombe Bottoms.

In the yew-wood at the head of Kingley Vale one or two gaps occur, which, although not formed by the death of old yews, are of special interest for our present purpose. In some, relicts of the original scrub and grassland are found, but owing to rabbit activity on the steep slope much of the soil is bare and unstable. The following plants are found:

<i>Atropa belladonna</i>		<i>Myosotis arvensis</i>	o.
<i>Bryonia dioica</i>		<i>Plantago major</i>	o.
<i>Sambucus nigra</i>		<i>Prunella vulgaris</i>	l.f.
<i>Arenaria serpyllifolia</i>	l.f.	<i>Sedum acre</i>	r.
<i>Cirsium palustre</i>	l.	<i>Urtica dioica</i>	l.
<i>Fragaria vesca</i>	o.	<i>Viola hirta</i>	l.f.
<i>Galium verum</i>	o.	<i>V. sylvatica</i> (agg.)	o.
<i>Lotus corniculatus</i>	+		

In 1922 yew seedlings were recorded as frequent, but in July 1923 only one was found, the seedlings having disappeared from gaps where the light is intense enough for survival. No young yews were observed. Thus yew regeneration is effectively checked.

The effect of rabbits and wind upon the establishment and growth of juniper and yew are clearly demonstrated in the woody vegetation colonising the wind-swept slope of the steep eastern spur of Kingley Vale (Pl. IV, Phot. 1, and Fig. 2). Here the scrub is open and consists solely of yew and juniper, the other shrubs being apparently unable to grow here. Both plants are wind-trimmed and in greater degree towards the north-east corner of the Vale. The juniper probably suffers more than the yew, for in the most wind-swept corner scattered, lopsided yews are found with no living, and rare or occasional dead juniper.

Almost every yew is growing along with a living or a dead juniper. Most of the yews are small—12–18 in. (30–45 cm.) high, often very small—4–7 in. (10–18 cm.), are closely nibbled, conical in shape and old. A small yew 7 in. (18 cm.) high showed approximately 55 growth rings.

The inference to be drawn from this and the previous observation is that

yew and juniper are the most wind-resistant elements of scrub and that successful establishment of yew in grassland is conditioned by the presence of scrub protective against grazing animals. At the same time it may be questioned if the yew seedling can readily become established in a grassy turf, and its association with scrub elements may, in the first instance, be due to the provision round the bases of shrubs of suitable germination and establishment conditions, such as exposed soil or shade. Experimental proof is lacking, but the record of one seedling only from an enclosure made eleven years earlier and near to abundant yews strengthens the suggestion. This seedling, too, was found in the "deep shade of *Crataegus*"¹; according to some observers the yew seedling is intolerant of strong illumination².

The conclusion that protective scrub is necessary for successful establishment of the yew is supported by observations from the juniper scrub in other parts of Kingley Vale, where the observed facts are similar to those just described: from the association of yew with *Crataegus* and *Prunus spinosa* at Stead Combe; with *Prunus* in Bottom "A," with juniper in Hillhampton and Wascombe Bottoms; and by the occurrence of inadequately protected and heavily grazed yews in all these localities³. Of the scrub elements, juniper is apparently the most effective to protect yew, and this is reflected in the more rapid colonisation of juniper scrub than of hawthorn scrub. This effective initial invasion means a rapid passage to yew-wood.

The view that yews are immune from attack by grazing animals is erroneous, for these small conical yews are trimmed down by such animals, probably by sheep, hares and rabbits. Rabbits also nibble the bark off stems and branches. Lowe⁴ states that "deer, sheep, goats, hares and rabbits eat yew without harm" and Elwes⁵ records that he has seen yew stems gnawed by rabbits.

The transition from the juniper to the hawthorn sere is recognised by the increasing frequency of *Crataegus* and a corresponding decrease in juniper. List 4 from the eastern slope of Wascombe Bottom indicates a transitional community. Here and in the more sheltered parts of the other localities juniper grows larger, and taller, has often a spreading habit and bears pale sickly foliage in contrast to the healthy appearance of large or small junipers in exposed communities. The physiological cause of this is unknown but soil factors evidently contribute to the production of the effect.

(b) THE HAWTHORN SERE.

This sere occupies the less exposed parts of the valleys. The difference in the habitat is reflected in the flora, for in the juniper sere there are only 22 species, while in the hawthorn sere there is almost twice that number—42.

¹ Tansley. *L.c.* 1923, p. 176.

² Hempel and Wilhelm. *Die Bäume und Sträucher des Waldes*, 1893, p. 200.

³ But see also p. 302.

⁴ *Yew-trees of Great Britain and Ireland*, 1897, p. 150.

⁵ Elwes and Henry. *Trees of Great Britain and Ireland*, 1906, 1, p. 119.

Of the 20 additional, most are local or have a low frequency. These, it is interesting to note, include *Ruscus aculeatus* which was not observed in exposed places: the evergreen *Ilex* is however equally widespread in both.

The two varieties of the hawthorn sere are separated on the basis of the presence or absence (or rarity) of ash. Floristically the two are similar, the sere without ash containing 35 species, the sere with ash 39. There are seven—*Acer campestre*, *Calluna vulgaris*, *Rubus idaeus*, *Ruscus aculeatus*, *Salix caprea*, *Ulex europaeus*, *Viburnum opulus*—not recorded from the sere without ash, whilst there are three—*Humulus lupulus*, *Pinus silvestris* (subspontaneous), *Prunus insititia*—not recorded from the sere with ash. All these species play a minor part in the vegetation in which the dominants are the same. Apart from the variation in the frequency of ash, the main difference is found in the relative frequency of the species common to both; *Clematis*, *Cornus* and *Rubus fruticosus* (agg.) are more frequent and *Ilex* more evenly distributed in the sere with ash, whilst *Prunus spinosa* is more frequent and *Rhamnus* more widespread in the sere without ash.

The Hawthorn Sere without Ash.

On the whole, the variety without ash is more exposed than the variety with ash. Exceptions occur; for example, the yew communities on the sheltered western slopes of Bottom "B," Hillhampton and Wascombe Bottoms; and exactly why ash is scarce in, or absent from these localities is not understood.

In the development from scrub to yew-wood the same stages are recognised as in the juniper sere and the process of invasion and succession is similar; only the differences need be emphasised here. The species are listed in columns 9-21.

The chief constituents of the scrub, *Crataegus* and *Prunus spinosa*, are accompanied by a number of shrubs whose frequency varies much in different localities. In the Butser Hill examples there are only 15 species, all, except the dominants and yew and elder, with a low frequency, but in Stead Combe (Fig. 3, 9) and Kingley Vale (Fig. 2, 14) there are 25 species including many of the commoner "chalk" scrub elements, some with a high frequency—*Euonymus* (f.), *Ligustrum* (a.), *Rosa micrantha* (f.). A similar difference is noted between the richness of yew scrub from Holt Down (Fig. 4, 15) and Kingley Vale (Fig. 2, 18) (29 species) and the poverty of the same stage from Butser Hill (14 species). These differences are emphasised by the accompanying grassland which near the Butser Hill examples contains much less *Poterium sanguisorba* than in the other localities, where this species is conspicuous. The probability is thus indicated that the present grouping includes habitats whose soils are really different.

The association of yew and hawthorn in this sere is much less common than that of yew and juniper in the juniper sere. This is due to the lesser ability of the hawthorn to shield invading yews so that not only are yew

families fewer in number but they enlarge much more slowly. That they are progressive is shown by the dead remains of *Crataegus*, *Clematis* and *Rubus fruticosus* (agg.) found under the yews. Thus yew scrub and the developing yew-wood belonging to the hawthorn sere are much opener than the corresponding stages of the juniper sere, the large and small yew families being separated by gaps, which, in rabbit-infested areas, bear a scattered scrub, a crisp turf, rabbit-immune herbs or no vegetation at all. The establishment

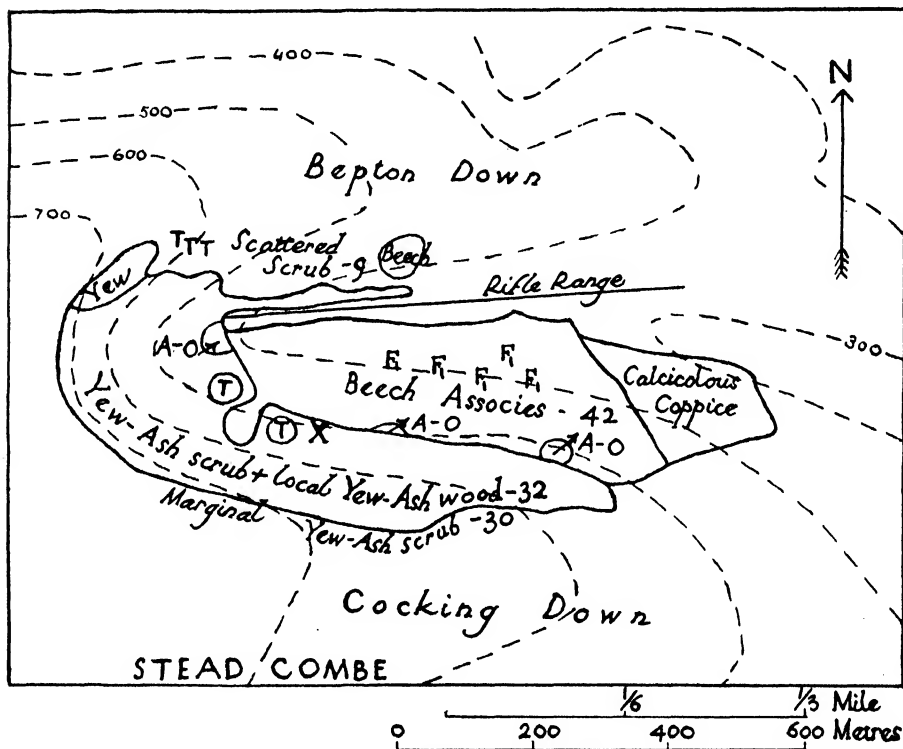


FIG. 3. Sketch-map of Stead Combe showing distribution of the "yew system" and the "beech system." A very old yew grows in the position marked *X*; pure yew-wood is local marked *T*. Five old pioneer beeches grow in the positions marked *F*₁. The ash-oak associates has been almost entirely obliterated by the beech associates advancing up the slope; patches (*A-O*) remain.

of fresh yew families is therefore difficult and the approximation of the existing ones slow. Locally this may not be true, as for example in a large patch of "thicket" yew scrub on the eastern slope of Bottom "B," nor does it hold good generally of the yew scrub in Kingley Vale. This, however, is derived on its western side from juniper scrub and on the valley side from slowly fusing scrub clumps, and here the intervals between the yews contain a rich scrub. The general openness referred to is not observed in the final stage but the two examples from Kingley Vale (Fig. 2, 21) and Hillhampton

Bottom are of small extent and do not upset the conclusion based on the study of the preceding stages that the passage from scrub to yew-wood is typically much slower in the hawthorn than in the juniper sere.

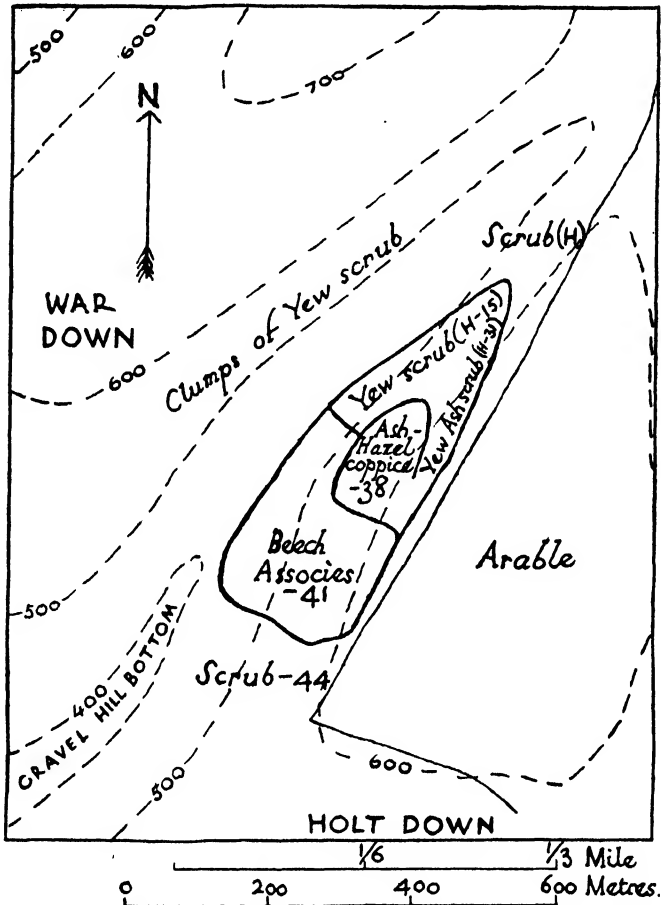


FIG. 4. Sketch-map of woodland on Holt Down, showing the distribution of the "yew system" and the "beech system." In the "yew system" ash grows only on the lee side. The ash-oak associates of the beech system is represented by ash-hazel coppice.

Changes in form and frequency accompany increasing shelter. Exposed and isolated blackthorn, hawthorn and yew are lopsided; in scrub, hawthorn frequency increases in clumps nearer the yew scrub, and in the yew scrub near the head of Bottom "B" attains a height of 25 ft. The frequency of *Clematis*, *Cornus* and *Rhamnus* is also greater in yew scrub and developing yew-wood than in scrub.

At the most, ash and oak are occasional and small except in one locality where ash is locally frequent. This is the northern margin of the developing yew-wood on the western slope of Hillhampton Bottom. Beech is recorded

only from the Stead Combe scrub where it grows isolated and in families, demonstrating the rapid transition from scrub to beechwood in exposed places¹.

In the yew scrub of Bottom "B," where there are no trees apart from the yew, there grows a patch of *Mercurialis perennis*.

The severe rabbit pressure is demonstrated in the Butser Hill examples by the large areas of bare soil with a mobile rubble of chalk stones and flints, by patches of short grassy turf, and by the replacement of grassland by an assemblage of plants disliked by rabbits—*Senecio jacobaea*, *Cirsium lanceolatum*, *Urtica dioica*, *Teucrium scorodonia*, *Myosotis arvensis*². In addition, small (7–9 in.) heavily grazed bushy yews are found, and the shoots of *Crataegus* and *Prunus spinosa* are cut off. In this way beds of low-growing decrepit *Prunus spinosa* are formed. The activity of rabbits is not limited to shoots accessible from the ground but is pursued into the crowns of taller bushes (3–4 ft.), where the upper sides of branches are barked and young erect shoots cut across. This results in a flat or convex crown which can extend laterally but not, or very slowly, upwards. A keeper informed me that this was the work of rabbits during the winter months when food is scarce, but in September I collected fresh shoots lying on the ground below the bushes. Both *Prunus spinosa* and *Crataegus* are attacked in this way.

In this sere *Sambucus* is locally common, growing abundantly on loose soil cast up round rabbit burrows and fairly frequently on soils exposed by severe rabbit grazing: its unusual frequency in the examples from Butser Hill is correlated with heavy rabbit pressure. Although apparently immune to rabbit attack, *Sambucus* seems to have little power to extend or persist, and this localisation is probably connected with the requirements of seed germination and seedling establishment, because the absence of *Sambucus* from grassland cannot be attributed to rabbit activity. And the same may hold good for some of the herbs which replace degenerate grassland.

In these rabbit-infested areas attempts to colonise gaps by woody species other than *Sambucus* are largely frustrated, so that the openness of yew scrub and developing yew-wood and the slow fusion of yew families are readily understood. It is doubtful if under present conditions large areas of continuous pure yew-wood could be formed.

In the pure yew-wood in the north-east corner of Hillhampton Bottom the yew attains a height of 40 ft., and the average girth of six large yews is 8 ft. 3 in. (2.5 m.)—the largest measures 9 ft. 2 in. (2.75 m.). As in the juniper sere, the largest yews in the valleys grow at the head of the valley or in that part of the community nearest to it; the size decreases outwards along the slope. Thus the direction of movement along the slopes, indicated by the order of the developing communities is confirmed by the age of the yews.

¹ Watt. 1924, p. 182.

² For a fuller account of this kind of vegetation, see Tansley and Adamson. *L.c.* 1925, pp. 211–218.

At the head of Bottom "B" large gaps, occupied by turf, by rabbit-immune herbs and by a large colony of *Sambucus*, separate members of an apparently decadent scrub of hawthorn, sloe and yew.

The Hawthorn Sere with Ash.

In this sere the normal course of development to yew-wood is not interrupted by the entrance and subsequent elimination of ash; its presence merely delays the appearance of pure yew-wood. The following stages are recognised: scrub, yew scrub, ash scrub, yew-ash scrub, yew-ashwood, yew-wood.

These stages are identified from the most sheltered parts of Stead Combe (Fig. 3) and Kingley Vale (Fig. 2) and from the three slopes Downley Brow (Fig. 5), Chilgrove Hill (Fig. 6) and Holt Down (Fig. 4), where development takes place mainly away from the direction of the prevailing winds. Wind and rabbit activity are apparently the chief factors limiting the distribution of scrub, which is found best developed to leeward of the Downley Brow and Holt Down woodlands. In the similar position on Chilgrove Hill rabbit activity has denuded the narrow strip of steep slope between the woodland and an abandoned chalk pit now being colonised by a rich scrub. In the grassland of the lower slopes colonisation by woody plants is extremely difficult, as the work of Tansley on Downley Brow proves, so that the scrub forms a discontinuous fringe to the lower side of the woodland strips of Downley Brow (Fig. 5, 28) and Chilgrove Hill and along the upper exposed margin of Stead Combe (Fig. 3, 30). In Stead Combe this marginal scrub widens out on the more sheltered gently sloping and east facing part of Cocking Down, and along the upper margin of Downley Brow (Fig. 5, 29) and Chilgrove Hill (Fig. 6, 27) the scrub forms a continuous and wider zone. In the grassland of the lower slope of Chilgrove Hill (Fig. 6, 26) and in the valley bottom of Kingley Vale (Fig. 2, 25) scrub clumps of varying size and with or without trees are found.

The extent of the scrub sets limits to the successful establishment and spread of both ash and yew: young ash is indeed locally abundant in the grassland but is kept down by persistent grazing, and isolated yews suffer in the same way. Of these two trees, ash is the more mobile so that where scrub is extensive and conditions suitable ash colonisation precedes that of yew. This is exemplified on Downley Brow (Fig. 5, 24) and Chilgrove Hill (Fig. 6, 23) where an ash scrub stage precedes effective yew colonisation. On Holt Down, probably because of exposure rendering ash establishment difficult, yew scrub precedes the stage with ash, which even then appears on the lee side only (Fig. 4, 15 and 31).

On the other hand, where the scrub is of small extent and its spread extremely slow, as in the narrow fringing scrub and in the scrub clumps, no such fractional separation of the stages can take place and scrub passes

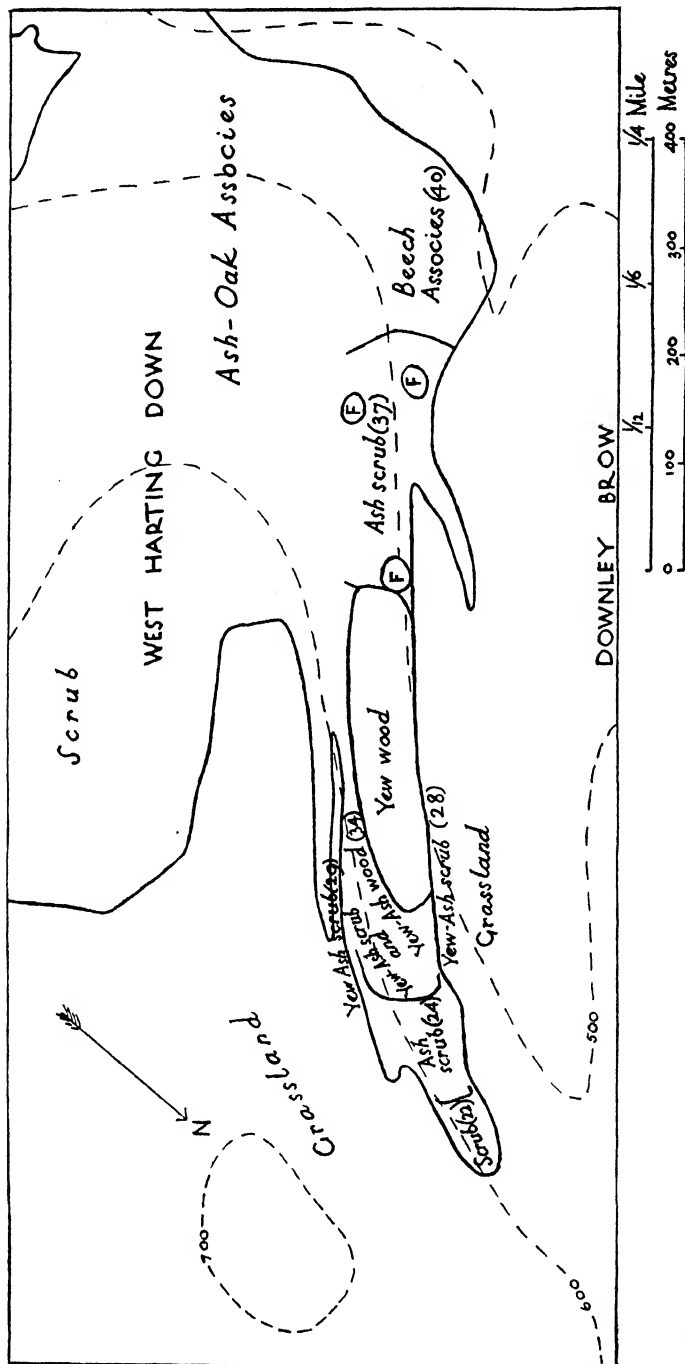


FIG. 5. Sketch-map of woodland on Downley Brow showing the seral stages in the development of yew-wood, and ash scrub and the beech associates of the beech system. Development is mainly to leeward. In the ash scrub occur degenerating groups (F) of old pioneer beeches. The beech system is continuous with the ash-oak associates (sere 3) of the plateau.

directly to yew-ash scrub. The effect is seen in the abrupt transition from grassland through a narrow zone of yew-ash scrub to a later stage with old yews and in the structure of scrub clumps consisting of yews encircled by a narrow scrub colonised by ash. That the rate of enlargement of some of these clumps is extremely slow is evidenced from the very large and old yews, the average girth of eight large trees being 14 ft. 8 in. (4.47 m.)—maximum 21 ft. 0 in. (6.4 m.). These still border on grassland or are hugged by a narrow scrub. Some of the larger clumps at Kingley Vale show development towards true woodland structure which is attained in certain clumps at Chilgrove, where there is a canopy of ash, a definite shrub layer, and a ground flora

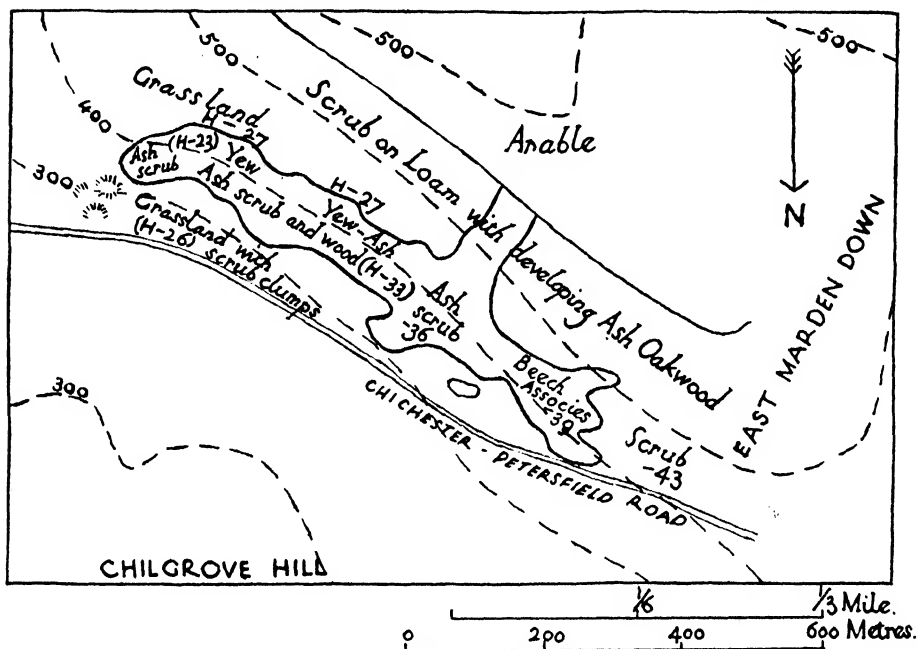


FIG. 6. Sketch-map of woodland on Chilgrove Hill showing similar distribution of stages found on Downley Brow.

dominated by *Mercurialis*. The zone of scrub along the upper margin of the Downley and Chilgrove woods is freely invaded by ash and yew but is too narrow to permit a separation of the ash scrub and yew-ash scrub stages, although ash is decidedly more frequent than yew along the forward margin.

The ash scrub consists of a hawthorn scrub freely invaded by ash which forms the canopy. The tangles of dead *Clematis*, *Crataegus* and *Rubus fruticosus* (agg.) indicate the change from open conditions to growth under canopy and demonstrate this ash scrub to be the early stage in the development of the ash-oak associates preceding beechwood¹. The only woodland herb is *Mercurialis* which is occasional to locally frequent, but no true ashwood with

¹ Watt. *L.c.* 1924, p. 164.

shade forms of *Crataegus* and with a woodland flora is found. This is prevented by the establishment and spread of the yew in the ash scrub, thus giving rise to the yew-ash scrub. Here, by the establishment and growth of young yews, and by the enlargement of existing yew families, the scrub is gradually suppressed, but the taller ash survives. The rate of development varies much. At Downley and Chilgrove the ash scrub is effectively colonised by yew which quickly suppresses the scrub, but at Stead Combe, where the yew-ash scrub (Fig. 3, 32) is extensive, the process is a slow one. This is apparently correlated with the openness of the hawthorn scrub, in which diffuse yew families and scattered yews occur. Here, too, there is a woodland flora dominated by *Mercurialis perennis*.

In the yew-ashwood most of the scrub has been suppressed, and the wood consists essentially of an upper diffuse canopy of ash and a lower of yew. This stage is identified from Stead Combe, Chilgrove (Fig. 6, 33) and Downley (Fig. 5, 34), but is best represented at Kingley Vale (Fig. 2, 35), where the yew-ashwood occupies the whole of the north-west corner.

The ash attains a height of 50–60 ft. (15–18 m.) and a diameter of a foot or more; some old stems lie rotting on the floor. The yews are of large and imposing size, up to 40–50 ft. (12–15 m.) in height and to 18 ft. 6 in. (5.64 m.) in basal girth—the average of 17 large trees at Kingley Vale being 13 ft. 2 in. (4 m.). By the death of some old yews gaps occur whose flora is described later (see p. 300).

The Kingley Vale yew-ashwood affords an excellent illustration of the extreme slowness of the fusion of yew families, for in the lower part of this wood relicts of the original scrub still survive between yews considered by Lowe to be 500 years old¹. In the upper and younger part of the wood the development has been much more rapid.

When the ash trees die, their replacement by young growth is prohibited by the shade of the yews; yew-ashwood passes to yew-wood. This appears locally in Stead Combe but is best developed on Downley Brow, where the canopy is almost pure. The derivation of the yew-wood from the approximation and fusion of yew families is evident from the arrangement of the smaller straight-stemmed yews round the larger pioneer forms; from the association of the surviving ash with the smaller yews; from the dead ash and hawthorn on the floor; and from the relicts of scrub in small enclaves.

The direction of spread is confirmed from examination of the size of the yews in different stages and in different parts of the same stage. On Chilgrove Hill, Holt Down and Downley Brow the size of the yew increases from the early stages to the last stage reached in the different localities; at Kingley Vale the oldest yews are found nearer the foot of the slope, and at Stead Combe the oldest yews, including one with a basal girth of 19 ft. 9 in. (6 m.), grow near the boundary between the yew community above and the beech-

¹ *L.c.* p. 60.



Phot. 1. General view of Kingley Vale, looking up the valley.



Phot. 3. General view of Hillhampton Bottom, showing yew-woods on the slopes and the yew relicts in the abandoned area near the head of the valley.



Phot. 2. General view of combes on Butser Hill, showing limitation of yew-woods to valleys. Starting from the right, Bottom "A," Bottom "B" and Hillhampton Bottom.



Phot. 4. Head of Hillhampton Bottom: in the foreground, part of the abandoned area; in the centre, two ash trees in yew-ash scrub clumps; on the sky line, hawthorn scrub with yew invaders on loam.

wood below, in the position marked *X* in Fig. 3. In all these invasion has taken place outwards from the oldest yews; faster along the slopes than up and down and faster up than down; in the valley bottoms faster up than down.

While ash, oak and beech are unable to grow under a yew canopy, they may colonise the intervals between yew families in the developing yew society and may become locally dominant there. In this last case development may proceed to maturity, when the colony exhibits true woodland structure and is to be considered an outlier of woodland. The relation of the yew to these will be considered in the next section. Meantime attention is directed to isolated trees or groups of trees which form patches of developing woodland within the developing yew society.

Two facts are relevant here: the longevity of the yew and its dependence on scrub. So long as scrub grows in the intervals between yew families the yew can colonise readily and gradually fill up the gap. This process is well illustrated in the development from scrub to yew-wood just described, in which the long-lived yew utilises and then suppresses the scrub of the ash scrub and then outlasts the ash. In this way pure yew-wood is formed. The same may apply also to oak although oak is rarely found in the developing yew-woods. With beech the case is different, especially if it has a pioneer form and grows in groups, as for example at Chilgrove and Stead Combe. The shade cast by the beech kills out the scrub and hinders yew colonisation and even if yew does become established the saplings often die or show poor growth and few leaves. It is doubtful if this colonisation is really effective. The beech is unable to regenerate and the surrounding long-lived yews still survive when by the death of the old beeches a gap is formed. This will not usually be occupied by the yew until scrub first becomes established. Groups of beech may in this way hinder the development to pure yew-wood.

THE DEVELOPMENT OF WOODY VEGETATION IN THE VALLEYS.

A separation between the seres has been made to trace the development of the different kinds of vegetation, but it has been shown that the two hawthorn seres and the juniper sere may contribute to the formation of a valley yew-wood; all three types of sere contribute to the yew-wood of Kingley Vale.

Photographs 1 and 2 (Pl. IV) show the striking limitation of the yew-woods to the valleys. This is due to the absence of scrub in the adjoining plateau grassland, but where the soil is deeper with superficial loamy deposits a hawthorn scrub is found, in which yew readily becomes established (see Pl. IV, Phot. 1 and 4, Figs. 1 and 2). In the bottoms of narrow valleys scrub and yews are absent owing to the intense rabbit grazing there.

From a study of the ages of the yews in the valleys as a whole it is found that the oldest yews grow near the head of the valley in the part most sheltered from the prevailing winds and that the age decreases outwards with distance from this point. This is true of all the valleys. It is thus believed that yew

colonisation first began here in a scrub of the hawthorn type and spread outwards, the scrub forming an advancing zone under the shelter of the progressing yew-wood and changing its character as the environment changed; in the more exposed parts hawthorn scrub is replaced by juniper scrub.

Juniper scrub may form a separate centre for yew invasion, as on the eastern spur of Kingley Vale and on the eastern slope of Hillhampton Bottom, where, locally, development has proceeded through yew scrub, developing yew-wood to pure yew-wood. At Hillhampton Bottom the interval between this outlier and the yew-wood in the north-east corner has been occupied by a juniper scrub which has succeeded rapidly to developing yew-wood by the free invasion of yew.

In any one sere the oldest yews are found in the most advanced stage represented in a valley, and not in the most advanced stage of development represented irrespective of sere. Thus the yew-ashwood at Kingley Vale contains the oldest yews on the slopes but it is flanked by pure yew-woods which, although distinctly younger, have nevertheless attained the final stage in their respective seres.

It is where the yews are oldest that degeneration begins.

DEGENERATION OF YEW-WOODS.

Three stages in the process may be described: failure to recolonise gaps formed by the death of old yews; disappearance of the yew-wood except for some relicts; abandonment of the area.

The difficulties attending the colonisation of primary gaps by yew and ash have already been pointed out and the same is true of gaps formed by the death of old yews. This is best illustrated in the yew-ashwood at Kingley Vale where a snowstorm in the winter of 1913-14 is reported by Mr Collie, the late forester at Goodwood, to have caused much damage, uprooting large and some small yews and breaking the branches of old standing trees. The gaps formed are bare or are colonised by a flora of special interest. The following are the species recorded from 13 gaps:

<i>Atropa belladonna</i> in 5 gaps	<i>Carex glauca</i>	+
" " seedlings l.a.	<i>Cirsium palustre</i>	+
<i>Bryonia dioica</i> in 4 gaps	<i>Fragaria vesca</i>	o.—l.f.
<i>Cornus sanguinea</i> in 1 gap	<i>Myosotis arvensis</i>	o.
<i>Clematis vitalba</i> seedlings in 3 gaps	<i>Mercurialis perennis</i>	l.d.
<i>Fraxinus excelsior</i> , one- and two-year seedlings	<i>Prunella vulgaris</i>	o.
" " two young plants in 1 gap	<i>Senecio jacobaea</i>	o.
<i>Hex aquifolium</i> in 2 gaps	<i>Sonchus oleraceus</i> (seedlings)	l.f.
<i>Taxus baccata</i> , one seedling	<i>Urtica dioica</i>	l.d.
" " one plant 6 in. high, nibbled	<i>Verbascum nigrum</i>	+
<i>Sambucus nigra</i> in all 13 gaps	<i>Veronica chamaedrys</i>	o.
	<i>Viola hirta</i>	o.
	<i>V. silvatica</i> (agg.)	o.—l.f.

Mosses are well represented in species but have difficulty in maintaining a foothold owing to rabbit activity.

The list shows that neither ash nor yew is successfully colonising the gaps formed. Only two ash plants older than 2 years were found, the majority of seedling ash being eaten by rabbits, as were also the yews, one of which, growing up in the fork of a superficial branched root, had temporary protection but is now closely nibbled. There is no establishment of a scrub fit to protect the seedlings; only the relatively immune *Bryonia*, *Atropa* and *Sambucus* being at all well represented. *Sambucus* is present in all the gaps and dominant in some.

There is an abundance of yew seeds on the floor of the wood, but the vast majority are without kernels. Some of the seeds have been split into two equal halves, but many have holes with ragged edges cut in them. The seeds are believed to be split by tits and the ragged holes made by mice¹, but both observations lack experimental verification.

The beginnings of degeneration at the head of Bottom "B" are demonstrated by the large gaps occupied by abundant *Sambucus* and rabbit-immune herbs; a later stage is seen at the head of Hillhampton Bottom (Pl. IV, Phot. 3 and 4, Fig. 1). This area is heavily rabbit-grazed. Herbs avoided by rabbits predominate, but on part of the western slope these are replaced by a crisp grassland over which loose chalk rubble is slipping down the slope. The woody vegetation is represented by two groups of clumps separated by a zone almost without woody plants. These groups adjoin the woods of the eastern and western slopes respectively. In both cases the clumps are dominated by yew families accompanied by a scrub of the hawthorn type. Some of the clumps are progressive as the dead remains of scrub under the yews show, although enlargement of the clumps is slow; but some families are without effective scrub elements and fail to extend. Some yew families indeed are represented by isolated old yews clear of branches 4–8 ft. up. In the clumps the oldest yews are of pioneer form and large size (the largest measuring 10 ft. 7 in. in girth). It is worthy of note that ash grows here, and in the adjoining developing yew-wood on the western slope this tree is confined to the zone next to the clumps just described.

Between the two groups of clumps lies the area of closely nibbled grassland in which grow one isolated hawthorn, two isolated sloes and three old yews. These yews are near the foot of the slope and girth 6 ft. 3 in., 7 ft. 3 in., and 9 ft. 0 in. The last two are clear of branches from 4–9 ft. up and on the first, large branches begin at 6 ft., but small epicormic branches grow out below (Pl. IV, Phot. 3, Fig. 1).

These three old yews as well as the isolated old yews near the developing yew-wood are considered to be the survivors of a community with yew and ash, which once occupied this part of the valley, the present distribution of ash marking the former bounds of this community.

¹ But see also **Kirchner, Loew and Schröter**. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*, 1, 1908, p. 77.

In addition to these detached yew clumps and large isolated yews bordering the northern margin of the yew-wood, developing clumps with young yews and isolated yews about 1 ft. in diameter, 10 ft. high and branched to the base grow on the western slope. These are considered as pioneers recolonising the abandoned area.

On the western slope of Hillhampton Bottom the oldest yews border on the area now almost abandoned, but in the woods of both slopes of Wascombe Bottom the oldest yews grow near, but not on, the north-west margin and are separated from the abandoned area by a narrow belt of almost continuous yew contiguous with the main body.

At the head of Wascombe the vegetation consists mainly of herbs avoided by rabbits. On the western part two areas of grassland with much moss are found, one adjoining the yew-wood the other on the slope of the western arm of the bifurcating valley head. Woody plants are represented by the following:

<i>Atropa belladonna</i>	l.f.	<i>Sorbus aria</i>	r.
<i>Bryonia dioica</i>	o.	<i>Rhamnus catharticus</i>	o.
<i>Cornus sanguinea</i>	l.	<i>Rubus fruticosus</i> (agg.) dead	r.
<i>Crataegus monogyna</i>	o.—f.	<i>Sambucus nigra</i>	f.—l.d.
<i>Prunus spinosa</i>	o.	<i>Taxus baccata</i>	f.

These are found singly or in clumps: the larger clumps consist mainly of *Sambucus*. Many of the hawthorn bushes are old and thick-stemmed and the decrepit sloe is pruned by rabbits.

Taxus may grow singly or in company with *Rubus*, *Crataegus* and *Rhamnus* or may form small families. The yews vary in height from 1 to 20 ft., and are of pioneer form, branched from the ground. The diameters of the two largest were estimated at 21–24 in. It is of interest to note that on the eastern slope and just outside the yew-wood there grow within a radius of about 20 yds. nine young yews from 12 to 18 in. high—all untouched by rabbits.

Complete abandonment of the head of the valley and a later stage in recolonisation are demonstrated in Wascombe Bottom (Pl. V, Phot. 5, and Fig. 1, p. 286). The only evidence that yew-wood once occupied the head of the valley is that the oldest yews grow near the north-west margin and that general progression of the woody vegetation is south-eastward along the slope. Direct evidence has disappeared with the complete disappearance of the original community.

It is of interest to observe here that Bottom "B," Hillhampton Bottom and Wascombe Bottom demonstrate a series in yew-wood degeneration, which is probably related to the size of the valleys. For it is likely that the longer and more sheltered valley of Wascombe would be first colonised and the yew-wood develop earlier than in the smaller bottoms. These in turn show yew-woods in descending order of development—Hillhampton, "B" and "A" Bottoms.

The conclusion that the yew-wood has abandoned the head of the valley is supported by the distribution of the yews in the neighbourhood of Deep Combe and Malcombe (v. Fig. 7). Reference to the figure will show that the



Phot. 5. Head of Wascombe Bottom, showing part of the rabbit-devastated area abandoned by yew-wood. On the right appear yews recolonising the area.

[Tansley and Adamson, 1925, Pl. VI, Phot. 3.]



Phot. 6. Holt Down, showing open hawthorn scrub with yew invaders south of the beech associates.

[Tansley, *Types of British Vegetation*, Pl. XVIII b.]

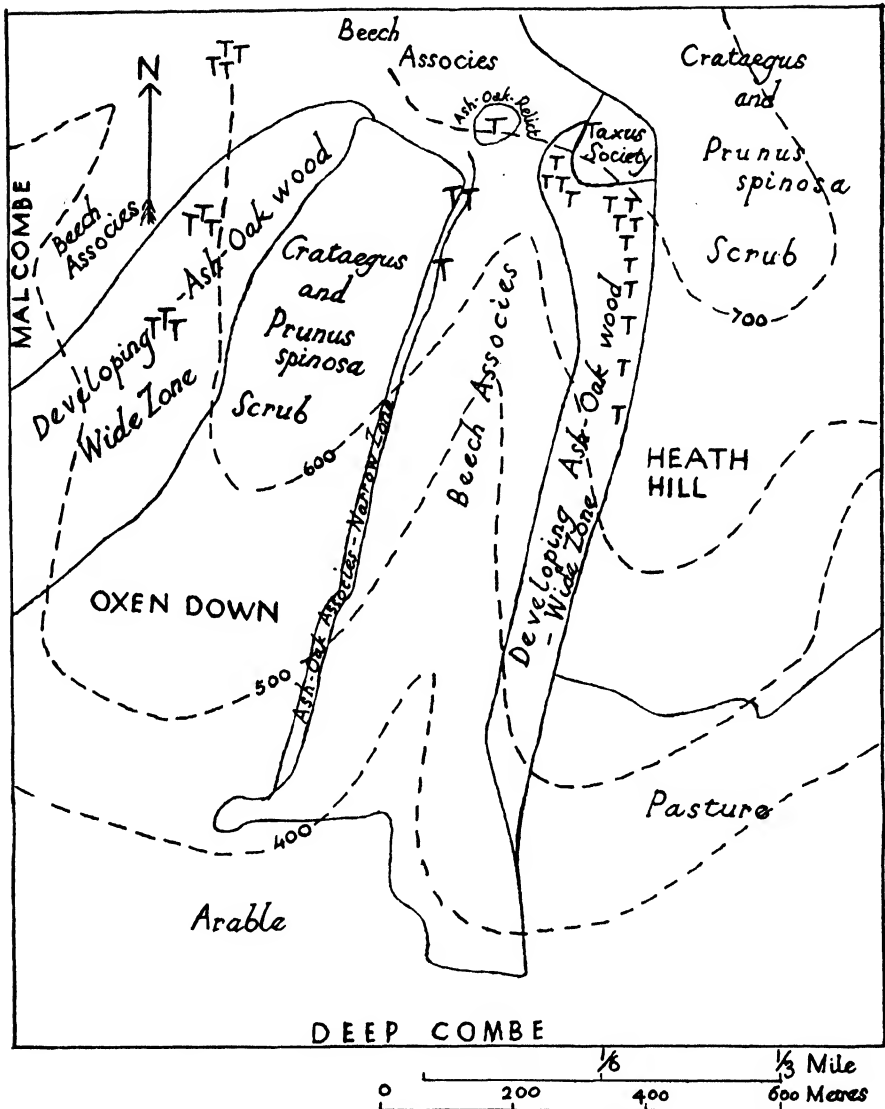


FIG. 7. Sketch-map showing distribution of woody vegetation round Deep Combe. The yew community has moved out from the valley, mainly eastwards and north-eastwards, and is now represented by the yew society and by abundant yews to the south of it in the forward zone of the ash-oak associates. The abandoned valley is now occupied by the beech system. Similar relations hold good in the adjoining valley of Malcombe.

yews occur round and above the head of Deep Combe and that the bulk of them are found eastwards of the valley. North-eastwards lies a *Taxus* society¹: elsewhere the yews are mostly scattered although patches of locally dominant yews are found. The structure of this society indicates progression eastwards. On the east and north-east margin the yew community is in the yew scrub stage with some older pioneers but many young yews. The average height is from 15–20 ft., and the average girth of 27 stems is 23 in. (extremes 13 in. and 48 in.). Behind, the yews stand less densely upon the ground and an easy passage can be made under the higher and closed canopy; the average girth of 29 stems is 34 in. (extremes 9 in. and 8 ft. 8 in.). In the ash-oakwood behind there is one yew family but the yews are mostly scattered; the tallest are from 35 to 40 ft., and the average girth of 29 stems is 48 in. (extremes 11 in. and 8 ft. 10 in.).

The distribution of the yews in the adjoining valley of Malcombe corresponds closely with that for Deep Combe. There is, however, no yew society although patches of locally dominant yew are found in the ash-oak associates east of the valley.

The evidence from Deep Combe shows that the *Taxus* community is migrating outwards from the valley—the main body travelling eastwards and north-eastwards. Here the abandoned area has been occupied by woodlands which have developed from scrub to ash-oakwood and beechwood.

SUMMARY OF SECTION I.

In this section the structure and development of several yew-woods on the South Downs are described, and evidence brought forward to show that these are migratory.

The yew meets with considerable difficulty in establishing itself in grassland. Perhaps ecesis in a grassy turf is difficult but the prevalence of closely nibbled isolated yews and the frequent association of yews with prickly shrubs suggest the efficacy of the animal factor in preventing successful yew invasion of grassland. This suggestion is supported by the close parallel between the degrees of susceptibility of prickly scrub elements to rabbit attack and the efficiency of these elements in promoting yew colonisation. Juniper is least attacked by rabbits and the association of juniper and yew is the most frequent. Hawthorn comes next in importance. For successful yew colonisation of grassland, scrub is essential.

The conclusion come to in a previous work that juniper and yew are the most wind-resistant of scrub elements is supported by the observations recorded here: hawthorn scrub is best developed in the most sheltered parts of valleys whilst a juniper scrub may be present on the exposed slopes as well as on sheltered slopes.

Two seres are recognised: a juniper sere and a hawthorn sere. Both culminate in pure yew-wood, but in the juniper sere the passage from scrub

¹ Watt. *L.c.* 1924, p. 167.

to yew-wood is rapid, whilst in the hawthorn sere it is much slower and may include intermediate stages with ash.

The size and height attained by adult yews decreases from the hawthorn sere with ash, through the hawthorn sere without ash to the juniper sere.

A comparison of the sizes of the yews in these valleys shows that the oldest yews grow in the most sheltered part and that size diminishes outwards. The juniper scrub may also form a centre from which the yews spread.

During development the yew kills out the scrub and forms a community, which, like the elephant herd, is socially well developed because of the longevity of the individuals. The vast majority of the yew seeds and seedlings are destroyed and when old yews die the re-establishment of a scrub protective of the few yew seedlings is prevented; the yew is unable to regenerate and the yew community dies out. This begins in the most sheltered part of the valley where colonisation first took place and spreads outwards leaving a gap where yew-wood once stood. A slow yew recolonisation of these abandoned areas is taking place.

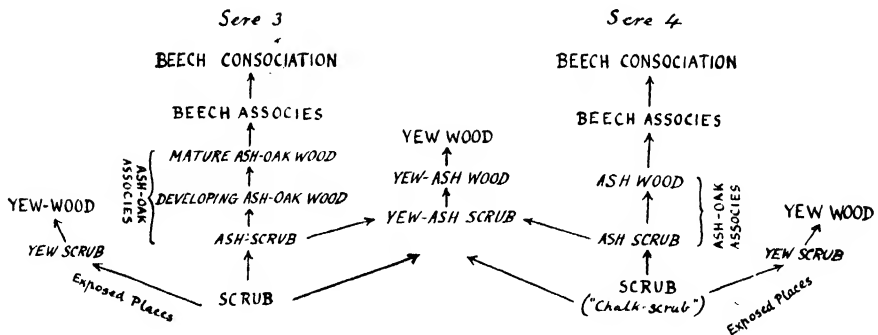
Ash, oak, and beech may grow in the intervals between the families of the developing yew society but because of the longevity of the yew and its capacity to endure shade, succession to yew-wood is not prevented, except sometimes perhaps by the beech.

As long as scrub maintains itself so long will the yew advance, and since hawthorn scrub is best developed to leeward yew advances most rapidly and abundantly eastwards, rather than westwards in the face of the prevailing winds.

Yew-wood is a single generation migratory community and owing to its dependence on scrub is best considered a society of scrub.

SECTION II. RELATION OF YEW-WOOD TO OTHER WOODY COMMUNITIES

The relationship between the two varieties of the hawthorn-yew sere and the normal succession of woody vegetation of seres 3 and 4¹ is presented schematically below.



¹ Watt. *L.c.* 1924.

In seeking to discover the relationship which the yew society bears to the normal succession, only the sere with ash need be considered since no direct evidence is obtained from a study of the variety without ash. By comparing seres 3 and 4 with the sere with ash it becomes apparent that the normal succession is arrested in the scrub or ash scrub stage by the spread of the yews, which by the formation of a closed society delay or check the invasion and development of ash-oakwood and beechwood. The relation of the yew to these later stages of the normal sere forms the subject matter of this section.

In the areas examined the full succession of each of the seres 3 and 4 is not seen, though stages representative of the general succession are found. No full treatment can therefore be given of the behaviour of the yew in the different seres of the South Down woodlands and while differences may be expected, they are probably not substantial as between the related seres 3 and 4.

The first requirement is a correct interpretation of the facts. For the woodland on Downley Brow an interpretation different from that of Adamson is given and my conclusion is supported from an analysis of similar woodlands on Chilgrove Hill and Holt Down. In these three areas I consider that we are dealing with two systems (designated briefly the *yew system* and the *beech system*) originating at some distance from each other on the same slope, with the beech system to windward of the yew system (see Figs. 4, 5, 6). To leeward of each the earlier seral stages are found. The generalised schemes of the two systems are as follows:

Yew system. Scrub, ash scrub, yew-ash scrub, yew-ashwood, yew-wood.

Beech system. Scrub, ash-oak associates (ash scrub, developing and mature ash-oakwood), beech associates, beech consociation.

The yew system was described in Section I. In no area examined is the full series of the beech system discovered but the evidence from the three woodlands mentioned previously is supplemented from Deep Combe and Stead Combe. Neither the scrub nor the beech consociation of the beech system has been observed in any of these areas.

THE BEECH SYSTEM.

Ash scrub. Between the yew system and the beechwood on Chilgrove Hill (Fig. 6, 36) and also on Downley Brow (Fig. 5, 37) is a zone occupied by an ash scrub similar to that already described as the first stage in the development of the ash-oak associates from scrub¹. It consists essentially of a hawthorn scrub freely colonised by ash with occasional trees of oak and beech, which on Downley Brow is also locally dominant. Most of the ash trees are young but a few are old. Old yews are occasional only (average girth of four trees on Downley Brow = 9 ft. 5 in.), and the yew families are largest and most

¹ Watt. *L.c.* 1924, p. 165.

frequent near to the yew system, becoming smaller and less frequent towards the beechwood. Hazel is a conspicuous shrub.

The origin of this ash scrub is clear. On Chilgrove Hill it consists of isolated, fused and fusing clumps of scrub with much young ash, separated in parts by enclaves of grassland. In the practically continuous and older ash scrub on Downley Brow the evidence is not so obvious, but in one gap were found *Gentiana amarella*, *Thymus serpyllum* and some grasses. These enclaves and relicts of grassland point to the superseding of grassland by scrub in which ash has become freely established.

On Downley Brow two gaps occur: one is due to the death of an old beech and bordered by two surviving and younger beeches, and now bears some *Sambucus* and *Rubus idaeus*; the other, formed by the death of two old beeches round whose stumps grows a scrub of *Rubus fruticosus* (agg.), *Cornus*, *Viburnum lantana*, *Clematis* and *Sambucus*, is now colonised by sapling ash.

In the Downley ash scrub there have been at least four beech clumps; two of these are noticed in the preceding paragraph; the third consists of a pioneer 20 ft. in girth at 3 ft. from the base, encircled by a number of semi-pioneers; the fourth is described in more detail. It is situated near the boundary between the yew system and the ash scrub and consists of six old beeches, five of which have the form of pioneers and one of a semi-pioneer. One pioneer is dead. Two survivors measured 15 ft. 4 in. and 16 ft. 4 in. in girth at 3 ft. from the base and are without doubt old trees. Under the beeches there are no shrubs, not even yews, but *Mercurialis* is occasional and small nibbled ash plants are frequent. The clump is closely surrounded by shrubs of which *Taxus* is dominant, but none of the encircling yews are large and all are clearly younger than the beeches.

Ash-hazel coppice. The ash-scrub in the two previous localities is replaced on Holt Down (Fig. 4, 38) by a coppice which is completely enclosed, on the north by yew scrub and yew-ash scrub and on the south by beechwood. Standards of comparatively young ash, beech and yew are found distributed in the coppice of hazel and ash: hazel (some probably planted) is dominant next to the yew-wood, and ash next to the beechwood. Here also grow *Sorbus*, *Sambucus*, *Euonymus* and *Clematis*, but with a low frequency.

Developing ash-oakwood. Flanking the beechwood in Deep Combe (Fig. 7) the ash-oak associates occurs—a narrow zone to the west, a wide zone of developing ash-oakwood (sere 3) to the east. Similar relations obtain in the adjoining valley of Malcombe, but here the ash-oak associates to the west is represented by a line of relicts on the beech associates of the plateau above. The developing ash-oakwood to the east of Malcombe belongs to sere 2. The structure, origin and development of these woods have already been described¹.

In the developing ash-oakwoods the yew has a varying frequency (occasional to frequent to locally dominant). All ages are represented from young yews

¹ Watt. *L.c.* 1924, pp. 160–176.

11 in. in girth to old yews 8 ft. 10 in. in girth. It is clear that regeneration is not prevented; but it is weak, and local dominance is due to older yews almost certainly established in the scrub or ash scrub which preceded the developing ash-oakwood. It is also significant that the yew is most frequent along the forward margin of the developing ash-oakwood (Deep Combe) where the wood is in a late ash-scrub stage. Immediately behind the yew society the yews are scattered except for one yew family. There is however no evidence to prove that the old yews represent the relicts of a once continuous yew-wood which has opened out with age and allowed the succession to ash-oakwood.

Mature ash-oakwood. Along the boundary between the yew-ash and beechwood at Stead Combe (Fig. 3) the ash-oak associates is represented by relicts; for the most part beechwood presses hard on the yew-ash scrub and yew-ashwood. Brief reference is here made to three of these relicts. Near the eastern end an enclave in the upper margin of the beechwood is dominated by *Fraxinus* and *Mercurialis* in their respective layers, the shrub layer being represented by occasional *Crataegus*: there is no *Taxus*. Midway along the slope there is an enclave dominated by *Quercus robur* and again there is no yew. But this associates is best represented in the south-west corner of the valley at the foot of the slope and adjoining the beechwood. The following are the chief woody plants and herbs:

<i>Acer campestre</i>	o.	<i>Quercus robur</i>	a.
<i>Cornus sanguinea</i>	o.	<i>Taxus baccata</i> (all comparatively young)	o.
<i>Corylus avellana</i>	o.	<i>Dryopteris filix-mas</i>	o.
<i>Crataegus monogyna</i>	o.	<i>Fragaria vesca</i>	f.
<i>Fagus sylvatica</i>	o.	<i>Mercurialis perennis</i>	d.
<i>Fraxinus excelsior</i>	d.	<i>Oxalis acetosella</i>	f.
<i>F. excelsior</i> (young)	l.a.	<i>Viola hirta</i>	o.
<i>Ilex aquifolium</i>	o.	<i>V. sylvatica</i> (agg.)	f.

The structure is that of a mature ash-oakwood. Yew is occasional, but despite the proximity of old yews there are no old plants here.

Beech associates. Beechwoods in the associates stage are found on the windward side of the woodland strips on Chilgrove Hill (Fig. 6, 39), Downley Brow (Fig. 5, 40) and Holt Down (Fig. 4, 41); on the lower part of the southern slope of Stead Combe (Fig. 3, 42); and in the valley bottoms and neighbourhood of Deep Combe and Malcombe (Fig. 7). The beechwoods in the first three localities are little more than very large clumps.

The structure varies considerably in the different localities, and with the dominant beeches there grow ash and oak varying in amount according as the associates is in an early or a late stage. On the exposed slopes enclaves may be filled with a scrub colonised by secondary and dependent ash¹, which on Holt Down is coppiced. The shrubs and ground flora vary with the canopy.

All forms of the beech, from aged pioneers to young erect stems, are represented; young stems predominate in the developing associates, but on Holt Down most of the trees are old. The "parents" of the Stead Combe

¹ Watt. *L.c.* 1924, p. 160.

wood are probably five very old dead and dying pioneer beeches found along the slope about the middle of the wood; and of the Downley Brow wood two old pioneers (17 ft. 3 in. and 12 ft. 10 in. in girth at 24 to 30 in. from the base) growing near the southern margin. Pioneer oak and ash are also occasionally found.

In all cases the direction of spread is mainly towards the yew system. This is confirmed from the occasional beech invaders in the ash scrub of Chilgrove Hill and Downley Brow, and in the ash-hazel coppice of Holt Down; and from the included ash and oak along the boundary between the beechwood and the yew-system of Stead Combe.

North-east of Malcombe yews are occasional to locally frequent in the young beech associates; elsewhere in the late beech associates in the neighbourhood of Deep Combe and Malcombe they are sporadic or even absent, despite the proximity of fruiting yews. Frequently those that are found grow near and under the immediate canopy of ash or where the beech canopy is more open. In the beech associates of the other areas yews are frequent.

The yew trees vary much in form and condition. Occasionally old pioneers are found, as for example locally in the forward margin of the beech associates in Stead Combe, where the old yews have been included, and near the southern edge of the Downley beechwood, where two pioneers grow measuring 9 ft. 1 in. and 9 ft. 5 in. in girth; but the majority of the trees are young and have obviously grown up under the beech canopy. These young trees are for the most part spire pointed, diffusely branched with scanty foliage—the leaves persisting on the secondary branches about 4 years only, and although surviving longer on the main branches are scattered. Under richly branched beeches occasional yews are flat topped, while under pioneer beeches no young yews grow. The young yews are obviously unhappy and whether they set seed is doubtful.

One instructive old dead yew was found in the late beech associates above Malcombe. It was about 2 ft. in diameter and of pioneer form but it had produced from near the base an erect stem which had grown to a height of about 30 ft. and a basal diameter of 8 in. This stem, an obvious accommodation to new canopy conditions, had also died.

Scrub. To windward of the beech associates on the slopes there grows a scrub which varies in composition but shows similar structure. It consists of isolated bushes and scrub clumps in which trees may or may not be established; yew is an invader in all areas. The Holt Down scrub is shown in Pl. V, Phot. 6. The beech associates is either not invading this scrub at all, as for example on Holt Down, or is pushing into it very slowly as on Chilgrove Hill and Downley Brow. These areas demonstrate the quick transition from scrub to beechwood of exposed slopes¹.

¹ Watt. *L.c.* 1924, p. 182.

THE RELATION OF YEW TO WOODS OF ASH-OAK AND BEECH.

The status of the yew communities has already been determined; it is a society of scrub. This does not exclude it from occupying a position in ash-oakwoods or beechwoods, but in this case the yew society is in them but not of them. For the case is quite conceivable, although a yew society in beechwood has not come under my observation, that the migrating yew society may be overtaken and surrounded by oncoming ash-oakwood and beechwood, and yet owe nothing to them for its establishment or maintenance.

In the woodlands examined we have seen that the yew society may originate in scrub or in ash scrub, but no example of establishment in developing ash-oakwood, mature ash-oakwood, beech associates or beech consociation has been observed. The later stages of the normal sere do not seem to favour yew society establishment. The relation of the yew to different kinds of woody communities will now be discussed.

Relation to scrub. This has been discussed; the yew society may develop here.

Relation to ash scrub. The evidence from Chilgrove Hill and Downley Brow shows that the yew society may also develop here.

Relation to developing ash-oakwood. In the developing ash-oakwood there is a breaking down of the typical scrub structure and a building up of the typical forest structure. Both in Deep Combe and in the adjoining Malcombe yews grow in this stage. Some are obviously included from scrub but some have grown up under the new conditions. These however show no definite movement towards the formation of a continuous canopy and the development of a true society. Yew may be a locally abundant constituent but local dominance is excluded, apart of course from the local dominance of a group of yews surviving from scrub or developed in ash scrub.

Relation to mature ash-oakwood. In the small areas of mature ash-oakwood in Stead Combe, yew is only an occasional constituent despite the proximity of abundant and old yews. In other woods previously described¹ yew may however be much more conspicuous; and is on the whole more frequent in sere 3 than in sere 2.

Relation to beechwood (beech associates and beech consociation). On p. 191 of the work cited the statement is made that as development of the beech associates proceeds the yew is gradually eliminated; and this is true of the beechwoods in the neighbourhood of Deep Combe and Malcombe. In the beech associates of Chilgrove Hill, Downley Brow, Holt Down and Stead Combe the frequency of the yew varies but is on the whole high. In the beech consociations of the plateau yew is infrequent and Adamson states that "in the majority of existing beechwoods *Taxus* is only an occasional tree²." In the "beechwoods on chalk" (sere 4) he further says, "The yew is present in

¹ Watt. *L.c.* 1924, pp. 165-171.

² Adamson. *L.c.* 1922, p. 209.

all of them, but is not abundant except in Head Down Hanger; in this wood the yew is locally subdominant and in the degenerate wood at Downley Bottom it becomes locally dominant¹." Regarding Head Down Hanger the following is a transcript from my notes made during a brief visit: "Much *Taxus*, mostly young. Middle aged yew dead under pure beech canopy but young yews surviving with few or short lived leaves."

The general condition of the yews varies with the density of the canopy. Between the normal healthy yews growing under an open canopy and the poorly developed flat-crowned yews under beeches of semi-pioneer form there are all transitions. Under richly branched and heavily foliaged beeches the yew is absent.

The shade-bearing capacity of the yew, the greatest among native trees, is pointed out by most writers, but according to Jaennicke² the tree is sensitive to long continuing shade; and according to my own observations the yew does not grow well under a *continuous and closed* canopy of pure beech. Exactly how long it survives is not known, but the majority of the yews observed are young. On yews growing under these conditions ripe fruits have not been seen.

Perhaps too much stress is laid upon shade as a factor limiting the growth of plants under woodland canopy. Root competition is an important and sometimes a deciding factor, but the yew shares with the beech the capacity to grow on shallow calcareous soils and its root system is probably as efficient as that of the beech.

The yew has a low specific conductivity (12 ± 2)³, but unlike *Ruscus aculeatus*, *Daphne laureola* and many conifers it can grow in dry places subject to drought: it is a soil xerophyte but not a dry climate plant. Conwentz⁴ reports that in the district of Heidenau, Bavaria, "shade" yews, when exposed by the removal of the spruce and beech canopy, were observed to sicken and die.

In the woodlands described here the yew attains larger dimensions in the hawthorn sere of deeper soils.

The example described of a yew which exchanged its pioneer form for the diffuse shade form to suit the new conditions is paralleled among scrub elements, for example by *Crataegus*, which is a bushy plant in the open but assumes the shade form under canopy. The death of "open" forms under shade and their replacement by shade forms either from the same stock or by new individuals is a subject requiring fuller investigation than has hitherto been accorded it.

A thicket scrub of hawthorn may be impregnable to trees, but under canopy there is no hint of *Crataegus* forming a definite closed society. *Taxus* seems to behave in a somewhat similar way, forming a society in the open,

¹ Adamson. *L.c.* 1922, p. 121.

² Jaennicke, quoted by Kirchner, Löew and Schröter. *L.c.* 1908, p. 62.

³ Farmer, *Proc. Roy. Soc. Ser. B*, 90, 1919, p. 218.

⁴ Conwentz. *Engl. Bot. Jahrb. Beiblatt* 46, 1912, p. 48.

but although sometimes locally abundant in woods of ash, oak and beech it seems unable to form a closed canopy under such conditions.

Yew regeneration is of course severely handicapped by animals which destroy the seeds and eat the seedlings and older plants. And this factor is undoubtedly important, though it is not offered as a full explanation of the inability of the yew to form a closed canopy in ash-oakwoods and beechwoods.

THE INTERPRETATION OF CHILGROVE HILL, DOWNLEY BROW, HOLT
DOWN, STEAD COMBE AND DEEP COMBE WOODLANDS.

Yew system. The development of the yew system has been discussed in Section I.

Beech system. On Chilgrove Hill, Downley Brow and Holt Down only two stages of the complete normal sere of woody communities are found, viz. ash scrub (and coppice) and the beech associates. The ash scrub of Chilgrove Hill still shows the clump structure and enclaves of grassland, that of Downley Brow is in a later stage of development but relicts of grassland occur.

The beechwoods of these slopes resemble the beech associates of exposed slopes in which ash and oak are secondary and dependent, filling up the intervals between the beeches. On the windward side the ash-oak associates is not developed on Chilgrove Hill and Holt Down but is represented by patches of ash scrub on the more sheltered southern end of Downley Brow. In all, invasion of the ash scrub and coppice to leeward is taking place.

The relation of the ash scrub to the beech associates is clear; the ash scrub is the early stage of the ash-oak associates developed to leeward of beechwood and compares in structure with ash scrub as described in previous work.

To leeward of the beechwood in Deep Combe the normal succession is found—scrub, ash scrub, developing ash-oakwood—but as yet sufficient time has not elapsed to allow the ash-oakwood to attain to maturity of structure. Locally the developing ash-oakwood is hemmed in between the yew society, which occupies the position of the ash scrub, and the beech associates advancing from the valley: in part the beech associates abuts directly on the yew society.

A later stage in this process of obliteration is demonstrated in Stead Combe, where for the most part the beech associates, probably derived from a few pioneers still extant, presses hard on the yew system. There is clear evidence to show that an ash-oak associates has been overcome by the beech associates advancing toward the yew-wood; relicts of mature ash-oakwood are found.

From these areas an almost complete normal sere of woody vegetation can be reconstructed. This is in conformity with the development of the woody vegetation described in previous work.

THE ORIGIN OF THE YEW-WOODS AND THE PLACE OF YEW IN THE
BEECH SYSTEM.

In only one of these five areas—Deep Combe—is there evidence to show that the yew society has migrated from its original position. Subsequent to its withdrawal the woody communities of the normal sere have originated in, and progressed outwards from, the valley.

In Stead Combe it has been shown that the oldest yews grow on the slope near the south-west corner of the valley. There is no evidence that yew-wood ever existed on the site now occupied by beechwood, and if scattered pioneer yews ever grew there they have quite disappeared. Difficulties in the way of yew establishment and extension were pointed out in the study of the woody vegetation on the floor of Kingley Vale, and the observations from Downley Brow and Chilgrove Hill emphasise these obstacles on the gentler lower parts of these slopes. To detail the exact course of the development of woody vegetation on the lower slopes of Stead Combe is impossible, but the evidence justifies the conclusion that a succession of hawthorn scrub, ash-oakwood and beechwood has taken place.

On the three slopes, Chilgrove Hill, Downley Brow and Holt Down, there is again no evidence to show that the yew-woods have withdrawn from their original position or are migrating as a whole along the slope. This simply means that the yew society is comparatively recently established and that the original colonists are still extant: that the yew society will migrate, under conditions similar to those existing, seems clear. That migration and subsequent colonisation by ash scrub and beechwood has taken place is negatived by the occurrence of scattered old pioneers in the beech system. These pioneers are old, but none are quite as large as the largest yews measured in the latest stage of development represented in the adjoining yew system; they are however of the same order of magnitude.

From internal evidence the early history of these woodlands can be reconstructed. In a hawthorn scrub scattered in the grassland of the slopes, appeared yew invaders. The scrub to leeward, benefiting from the shelter of that on the windward side, developed more quickly and allowed a more rapid growth of the yew families in the position now occupied by the largest yews. The increased shelter thus afforded by the wind-resistant yew promoted the spread of scrub to leeward and with it the extension of the yew, the growth of yew families and the differentiation of the seral communities.

The development of the vegetation windward of the yew system can best be explained by picturing the state of the vegetation before the establishment of the beech and the beech associates: this is materialised in the scrub south of the beech associates on Holt Down, which consists of a scattered hawthorn scrub with scrub clumps and yew invaders (Pl. V, Phot. 6). Since the position of this scrub was to windward, development both of the scrub itself and of the

yew families was very slow and quite old yews occurred scattered in the open scrub. The establishment of the beech and its subsequent development to woodland provided shelter and stimulated the growth of scrub, which rapidly filled up the intervals between the original clumps and permitted the growth and spread of ash, hitherto absent or rare in the exposed open scrub. The spread of the scrub allowed more rapid increase in the size of the yew families.

This hypothesis conforms to the known behaviour of ash, beech and yew and explains the distribution of old pioneer yews both in the ash scrub and in the beech associates. The frequency of hazel in the ash-hazel coppice is in conformity with its frequency in the ash scrub of the beech system.

On Downley Brow, in addition to the young beech invaders, there are four clumps. In these all the trees now living are old, of pioneer and semi-pioneer form, and have grown up in open conditions such as prevailed during the early stages of vegetational development windward of the yew system. In the open scrub with yews of that period, pioneer beeches had become established. Three of them at any rate have reproduced and formed a family, but no further extension has taken place. These clumps are degenerating, but they are not considered to be the remnants of an original beechwood but pioneer clumps which have failed to extend.

Of the woods considered by Adamson to be degenerate¹, two are included in the present account, viz. Oxenbourne Down (eastern slope of Wascombe Bottom) and Downley Brow. The Downley yew-wood he considers as having arisen from a beechwood from which the dominant trees have been removed or died and he finds in the degenerate beech clumps and in the presence of some woodland plants such as *Arum maculatum* and *Mercurialis perennis* evidence of previous continuous woodland cover. He also sees in the present distribution of the beech clumps the progression of destruction of the beech forest. The origin of the Oxenbourne wood is not so obvious, but he classes it along with the Kingley Vale yew-wood and considers both as a subclimax due to the destructive action of rabbits in large numbers.

The following criticisms of this view are offered:

1. The presence of *Mercurialis perennis* and *Arum maculatum* cannot be held as reliable evidence for the former existence of woodland because both occur in places reproducing woodland conditions, e.g. under scrub and by hedgerows.

2. On Downley Brow the beech clumps consist of trees showing pioneer or semi-pioneer forms which could only have appeared in open conditions. Further there is no relation between the supposed progression of beechwood destruction and the stage of development reached by the yew-wood.

3. The view does not explain the occurrence of old pioneer yews in the beech system: yews grown under canopy do not develop bush or pioneer forms.

¹ Adamson. *L.c.* 1922, pp. 206, 208-210.

4. The phenomena of invasion and succession are left unexplained.

5. On *a priori* grounds it seems possible that yew-woods could arise from beechwoods, but there is no good evidence to support this view: in fact, the evidence from the plateau woods shows that the yew tends to disappear from the later stages of the beech associates.

STATUS OF THE ADULT YEW COMMUNITY.

The preceding analysis shows that the yew loses its high sociability value in the woodlands leading to the beech consociation; in these, in fact, the yew community disintegrates.

The determination of the status of the adult yew community in the vegetation of the South Downs is based on the well-attested belief that the beechwoods are progressive. On the calcareous soils of areas not yet or but insignificantly invaded by the beech—the Downs east of the Arun, Butser Hill and much of the lower dip slopes of the western wooded area—grassland predominates, and scrub with yew societies is found in valleys and sheltered places. This is believed to represent the original condition of the vegetation in areas now wooded. Grassland is climax and the yew forms a society in post-climax scrub, growing in areas whose local climatic conditions favour the development of woody communities. On slopes similar favouring conditions are provided by the coalescent yew groups to leeward of which invariably occurs the main development.

On these calcareous soils formerly dominated by grassland the arrival of the wind-resistant beech provides the conditions necessary for the extension of scrub and woodlands of ash and oak. Although yews are found in this scrub of the main line of succession, there is apparently no time for the development of the yew society which is not normally found there. Occurrence within the main line, as at Deep Combe, is due to a society of the original scrub being overtaken in its migration by the faster moving ash-oakwoods and beechwoods, in which the yew society disintegrates. The yew society is therefore not a normal constituent of the succession leading to beechwood and in Clement's nomenclature is a relict society.

In summary we may say that the adult yew community is a society of the original post-climax scrub and a relict society in the succession culminating in the present progressive beechwoods.

SUMMARY OF SECTION II.

The analysis of five South Down woodlands shows that one part consists of a series of stages leading to pure yew-wood, the other to beechwood. These are called respectively the yew system and the beech system. In no one area are all the stages of the beech system found. The following is the generalised succession:

Yew system. Scrub, yew-ash scrub, yew-ashwood, yew-wood.

Beech system. Scrub, ash-oak associes, beech associes, beech consociation.

In four woodlands the yew system extends to leeward of the beech system; the fifth grows on a sheltered valley slope.

The structure and development of the yew system is described in Section I. It is believed that the yew-wood originates by yew invasion of a scattered scrub growing on a slope. Development and differentiation of the seral stages take place to leeward, whilst to windward the scrub remains in an open condition.

The beech system is believed to arise subsequent to the establishment of a protective woodland of wind-resistant beech. To leeward succession proceeds through scrub to ash scrub, developing and mature ash-oakwood, beechwood. The ash-oak associes may be artificially stabilised as coppice.

The relation of the yew to these woody communities is discussed. The yew society may arise in scrub and in ash scrub, but although yews may be locally abundant in developing and mature ash-oakwood and in beechwoods, there is no good evidence to show that a yew society can be formed there. The inability of the yew to grow well under a continuous and closed canopy of beech is pointed out.

Previous views on the origin of yew-woods are criticised chiefly on the ground that they fail to explain the phenomena of development described in this paper.

The fact that all the yew-woods described both in Sections I and II are remote from or on the outskirts of blocks of progressive woodlands of ash-oak and beech is evidence in favour of the interpretation put forward.

Grateful acknowledgements are due to Mr Tansley for criticising the manuscript and to the Carnegie Trustees for financial assistance in carrying out the work.

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THE VEGETATION AND RETROGRESSIVE CHANGES OF PEAT AREAS ("MUSKEGS") IN CENTRAL ALBERTA

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(With Plates VI-X, Folding Map, and six Figures in the Text.)

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INTRODUCTION

In the present paper the plant communities and certain retrogressive changes on small well-defined peat areas in the Edmonton district will be described, and the origin of the peat deposits discussed.

In Canada the term "muskeg" is applied to areas of peat covered with a certain type of vegetation. The term is practically synonymous with peat-bog. *Sphagnum* is usually a much more pronounced feature in the peat areas of Canada than it is in northern England and Scotland, and trees of small or moderate size frequently occur on these areas. These features often give a very different impression to the usually treeless areas of Northern Britain. Many plants are common over these areas in both countries, but in Canada *Ledum groenlandicum* takes the place of *Calluna vulgaris* as the dominant shrubby ericaceous plant. It will be convenient in considering the distribution and succession of the vegetation if a brief description of the topography and meteorology of the district is given first.

TOPOGRAPHY

All the peat areas to be described lie within 30 miles of Edmonton, on the last step of the plateau east of the Rocky Mountains, which rise about 200 miles due west of Edmonton. The general altitude varies between 2180 ft. (Edmonton) and 2500 ft., the country being gently undulating except along the main river valleys, which usually descend abruptly to 200 ft. below the plateau, with steeply sloping gorges where tributaries enter the main valley.

Reference to the map will show, to the east and south-east of Edmonton, areas in which lakes occur in great abundance, varying in size from Cooking Lake, 9 miles long and from $\frac{1}{4}$ to $4\frac{1}{2}$ miles wide, to small pools 300 ft. across. Over an area of 400 square miles there are several hundred lakes large enough to be marked on a scale of 3 miles to 1 inch, and the total number, including the smaller lakelets, is probably greatly in excess of this number.

Much of the lake country differs somewhat in topographical features from that found elsewhere. Little hillocks abound, seldom more than 15 or 30 ft. high, often connected by curving ridges with flat basins between, and it is in these basins of varying size that the lakes and muskegs occur. All this country lies within the 2400 ft. contour line and therefore forms a plateau about 300 ft. above the country eastward which drains immediately into the Saskatchewan Valley. None of the lakes is of any depth, the maximum in Cooking Lake being 18 ft. whilst most of them are from 6 to 12 ft., and may be described as flat-bottomed basins lying on drift. The general flora of the waters is prolific, members of the Cyanophyceae being abundant, with many diatoms, a general absence of desmids, and a scarcity of filamentous members of the Chlorophyceae (see List, pp. 331-2). The lakes are frequently bordered by a zone of Carices and Scirpi, backed by zones of willow or spruce.

METEOROLOGY

Very few data exist except figures for rainfall and temperature, and even these records are available only for a few stations, are often imperfect, and do not extend over many years.

The rainfall records for three widely separated stations, North Cooking Lake about the centre of the lake area, Rocky Mountain House, 90 miles south-west of Edmonton and 60 miles from the mountains, and Red Deer, 100 miles south of Edmonton, are given below.

Annual Precipitation (inches).

	1916	1917	1918	1919	1920	1921	1922	1923	1924
Athabasca	—	—	—	*	22.87	14.69	13.44	14.95	18.34
North Cooking Lake	—	—	14.58†	15.33	19.53	14.00	12.85	16.99	18.27
Red Deer	22.79	16.58	*	13.40	12.81	*	12.21	22.92	20.07
Rocky Mt. House	—	22.53†	18.95‡	*	*	—	9.56§	*	18.14

* Incomplete returns.

† Jan.-Feb. missing.

‡ Oct. missing.

§ July-Aug. missing.

The earliest records do not date back farther than 1916, and some years are so incomplete that they have not been included; in others which are less so, the months that are missing have been indicated.

It is impossible to draw any certain conclusions from these records except that the rainfall is about 15 in. per year in the lake region, at Rocky Mountain House about 18 in. and at Red Deer about 16 in. Much of this comes as snow during the winter months but varies from 6 in. or even less in some years to a total winter fall of 5 or 6 ft. in other years. We are indebted to Sir Frederick Stupart, Director of the Dominion Meteorological Service for these figures. The difficulty of maintaining continuous records in sparsely settled districts must be great, and this was much accentuated during the later years of the war. The need of more scientific study of meteorological conditions such as light intensities, evaporation, relative humidity and wind movements, is obvious, the more so as climatic conditions are more variable in the north-west of Canada than anywhere on the Continent.

Probably no year ever occurs when the muskegs are not frozen continuously between early October and the latter part of April. Activity of the vegetation is thus limited to five months of the year or even less. Owing to high temperatures and frequent unclouded skies during the growing season, temperature gradients in peat areas are extremely abrupt. Thus in June or July with a shade temperature of 90° F. at the surface of the muskeg, the ground may be frozen 18 in. below the surface, and in many of the muskegs in which there is little or no circulation of water, the layers 2 ft. below the surface remain permanently frozen. Since many of the muskegs are not more than 100 yds. in diameter and are surrounded by banks of dark alluvial soil covered with poplar and grassland and sometimes cultivated, no greater contrast of conditions or vegetation within a small distance could well be found.

During the winter, humidity is nearly always extremely low and although it may attain a high value for short periods in the summer, the mean value is usually small. As regards rainfall, humidity and temperature, the climatic factors are not those usually associated with rapid or extensive peat formation, and the retrogressive changes seen in so many of the muskegs would probably be more marked were they not frozen for about seven months in each year.

VEGETATION OF AREAS NOT COVERED WITH PEAT

The area under discussion lies near the northern boundary of the parkland that stretches across the central region of Alberta and is bounded on the north by coniferous forest and on the south by northern prairie, which differs essentially in climatic features and vegetation from the semi-arid prairie lying farther south. The parkland belt in the meridian of Edmonton is about 160 miles in width and extends 40 miles north of the Saskatchewan River. It may be regarded as a transition zone between the prairie and the northern coniferous forest. Originally this undulating plateau was fairly continuously

covered by various species of poplar and shrub thickets. The dominant tree is *Populus tremuloides* Michx. and although much has been cleared for agricultural land, probably the major part of the area is still tree-clad. Accompanying the dominant species of poplar are several others, *P. deltoides* March, *P. sargentii* Dode. and *P. balsamifera* L. being locally abundant. Thickets of *Salix* are frequent, and throughout the country may be found *Picea albertiana* G. Brown (the western form of *P. canadensis*) occurring either singly or in groups and frequently becoming the chief tree in the river valleys and ravines. The coniferous covering is greatly extended by the numerous muskegs in certain regions. The chief tree here is *Picea mariana* (Mill) B.S.P. (black spruce), although *Larix laricina* (Du Roi) Koch frequently accompanies it. Birch is not abundant and chiefly occurs on the sides of some of the valleys and on muskegs.

The flora of the poplar woodland consists of a number of shrubs, among which species of *Rhamnus*, *Lonicera*, *Ribes*, *Rosa*, *Alnus*, *Salix*, *Shepherdia*, *Eleagnus*, *Prunus*, *Amelanchier*, *Symphoricarpus* are most noticeable, while the ground flora includes *Linnaea*, *Disporum*, *Mertensia*, *Potentilla*, *Mitella*, *Pyrola*.

The contrast of this form of vegetation, so uniform over large areas, with the plants found on the muskegs is very great, and is accentuated by the small size of many of the muskegs and the very narrow transition zone—often only a few feet across—from one type to another.

DISTRIBUTION OF MUSKEGS

While the two areas mentioned have been selected for description it may be of interest to indicate briefly the main features of muskeg distribution over larger contiguous areas. Muskegs at various stages of development or retrogression are of course confined to the parkland and coniferous forest to the north and are quite unknown in the prairie regions. In the parkland there is a progressive increase to the north and to the west. The most southerly muskegs observed are in the region of Lacombe, 87 miles south of Edmonton, and thus approximately 33 miles north of the southern boundary of parkland, but farther west examples occur in a more southerly position. A marked feature is their constant association with regions of lakes.

The distribution of peat areas is not indicated on any topographical or geological maps, and for this reason any account of their distribution in such a wide stretch of country must necessarily be imperfect. Generally speaking, the areas increase in extent west and north-west of Edmonton and on approach to the coniferous forest, continuous areas many miles in extent are encountered. Some of these larger areas have a different vegetation and probably vary in their developmental history from the small basins in the Edmonton district, but nothing has yet been recorded regarding these features, and from a botanical point of view they are quite unknown. Peat-covered areas are

unknown in the Eastern Rocky Mountains, but in the foot-hill region north of the Edmonton parallel they frequently cover large stretches of country. Their association with moraine remains can be noted in all districts.

VEGETATION OF THE MUSKEGS

(a) COOKING LAKE DISTRICT.

Between Edmonton and the northern shore of Cooking Lake lies a succession of muskegs occupying small, shallow and sharply defined basins. A number of these have been examined and two representative types are described here. Owing to the scarcity of place names on the maps, all the muskegs are designated by serial numbers and are so referred to in this paper.

No. 1 occurs 9 miles south-east of Edmonton and its topography and general features are shown in Fig. 1 and illustrated in Pl. VI, Phot. 1.

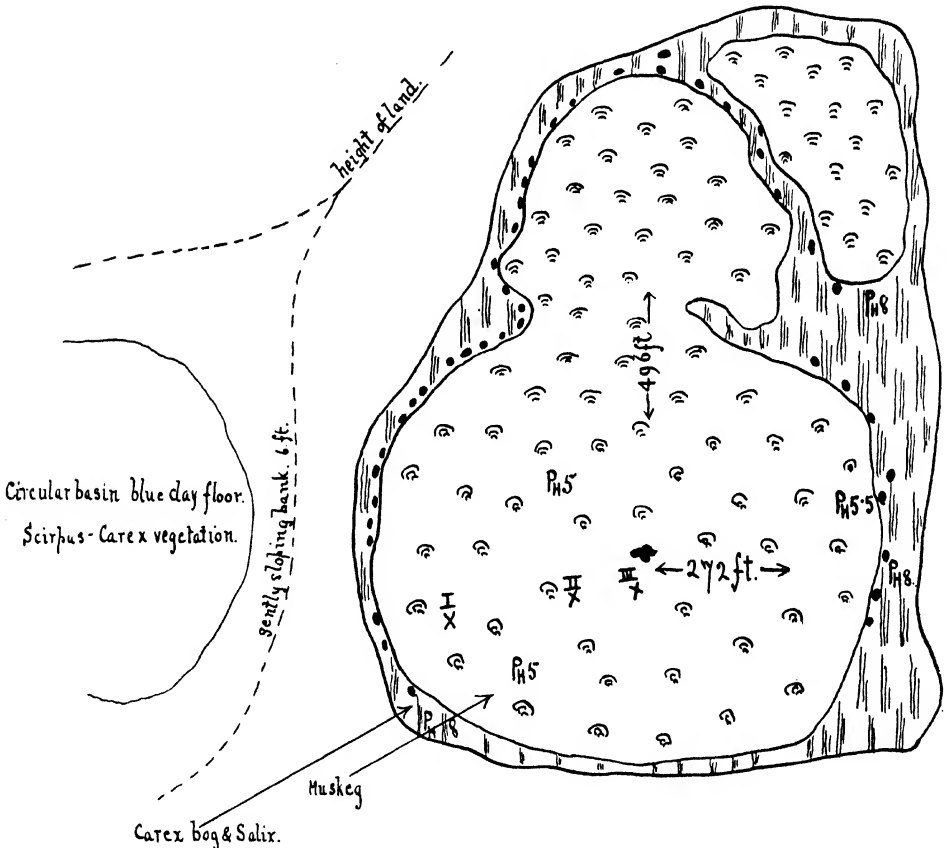


FIG. 1. Muskeg No. 1 in shallow clay basin surrounded by morainic banks.

P_H = Hydrogen ion concentration. For Vegetation, see Plate VI, Phot. 1.

The vegetation tends to be uniform and the dominant species are: *Ledum groenlandicum* Oedr., *Sphagnum acutifolium* var. *rubellum* (Wils.) Russow., *Vaccinium vitis idaea* L., *V. oxycoccus* L., *Rubus chamaemorus* L.

Subordinate species are: *Vaccinium canadense* Kalm., *Eriophorum vaginatum* Torr., *Vagnera trifoliata*, *Cladonia pyxidata* Hoffm., *C. rangiferina* Web., *Peltigera* sp., *Polytrichum commune* L., *P. juniperinum* Willd.

The growing centre of the muskeg consists of a small irregular extent of water a few feet across bordered by *Sphagnum* on which grow *Vagnera trifoliata*, *Vaccinium oxycoccus*, *Eriophorum vaginatum*, and *Larix laricina*. A few small patches of *Menyanthes trifoliata* occur in the pool, this being the only spot on the muskeg where this plant is found. This ecological centre is surrounded by mounds of *Sphagnum* somewhat drier in character, bearing *Ledum groenlandicum*, *Polytrichum commune*, larch and seedling birch.

The whole muskeg is dominated by actively growing *Sphagnum*, wet and spongy, forming mounds about 8 to 12 in. above the intervening hollows. Very little zonation of vegetation is to be seen, but as the outer zones of the muskeg are approached *Vaccinium vitis idaea* becomes relatively more abundant and *Vaccinium oxycoccus* decreases in amount. It will be seen from the sketch-map that the muskeg lies in a small basin and is surrounded by a border of *Carex* bog varying slightly in width, with a zone of *Salices* and *Alnus* close to the muskeg. The arrangement is symmetrical and the transition from the *Carex* bog to the sloping banks with *Populus tremuloides* and the usual ground flora is most abrupt. Borings were taken at several points marked on Fig. 1. The general depth of the basin is 8 ft. below the present surface of the muskeg, and the underlying material found in the borings is a stiff blue clay containing numerous grains of rounded quartz. This clay is described more particularly for Stony Plain muskeg. The peat immediately overlying the clay is not formed of *Sphagnum* and seeds and fruits of *Potamogeton* sp., *Menyanthes trifoliata* L., *Potentilla comarum* L. and *Carex* sp. have been collected from it. Thus the vegetation in this small basin was that of a shallow lake which in the course of time gave place to a peat bog vegetation.

Most of these muskegs are clad, to a varying extent, by fairly large trees of black spruce, birch and larch. This condition seems to have persisted for a long time as tree remains are found in this muskeg, as far as can be ascertained by borings, throughout the peat layer. Although the trees are relatively small, many are of considerable age and certain features connected with their rate of growth will be described in this paper. The present surface water has a pH 5 over the whole muskeg, but on the *Carex* bog only a few feet away from the margin of the muskeg values of pH 8 are obtained.

The topography in which this, and all other muskegs in this area occur calls for brief description. Everywhere are mounds and curved ridges enclosing small basins. The mounds and ridges are of slight altitude, usually about 10 to 30 ft. high and resemble well preserved morainic ridges and mounds.



Phot. 1. Cooking Lake, No. 1 Muskeg (pp. 321-2).



Phot. 2. Circular basin with floor of blue clay and *Carex* bog.



Phot. 3. Margin of Cooking Lake Muskeg No. 2. Raised muskeg to left and abrupt descent to surrounding *Carex* bog (p. 322).

The material of which the ridges are formed, however, is a yellow clay in which occur scattered boulders of great size. The clay underlying the muskegs in the basins is dark blue-grey with rounded quartz grains, from mere specks to about 5 mm. in diameter. The system of mounds and ridges and the material of which they consist, suggests deposition by water action at the retreat of the ice-sheet.

No. 2 muskeg occurs about half a mile east of No. 1. Its area is about the same, but important retrogressive changes have taken place. The whole muskeg is closely covered by *Ledum groenlandicum* with *Sphagnum*. The flora is essentially similar to that of No. 1 but the relative abundance differs, inasmuch as *Sphagnum* shows disintegration, particularly on the southward side of the mounds. Seedling trees do not occur in such abundance, and plants associated with the active growth of *Sphagnum*, such as *Vaccinium oxycoccus*, are not so frequent. The salient feature consists in the distribution of vegetation types in the small basin in which the muskeg is situated. The muskeg is surrounded by a zone varying from 20 ft. to 100 ft. of *Scirpus* bog and exists as a platform raised about 3 ft. above the encircling *Scirpus* zone. The border in some places is abrupt and the banks steep, but on the south margin, where the *Scirpus* zone is broadest, the muskeg is scattered and occurs as isolated patches separated by channels of *Scirpus*. The flora of the isolated muskeg mounds consists of *Eriophorum vaginatum*, *Scirpus caespitosus* with *Ledum groenlandicum*, *Polytrichum commune* and a slight amount of *Sphagnum*.

The broad zone of *Scirpus-Carex* bog, the raised platform of muskeg within, the scarcity of *Sphagnum* and the dominance of *Ledum* over the whole peat area, are the chief features of interest in this area.

(b) LOOMA DISTRICT.

This region is intersected in all directions by a network of small shallow lakes containing luxuriant vegetation which appears to consist mainly of *Utricularia intermedia* Hayne, *Potamogeton* spp. and an algal flora of which members of the Cyanophyceae—particularly *Nostoc*—are the chief constituents. It is difficult to examine the flora of most of these lakes as they cannot be approached during the summer owing to their being surrounded by a margin some hundreds of feet wide of liquid peaty clay more than 10 ft. in depth. Shallow basins of smaller size and tending to be circular in outline are occupied by muskegs. The whole topography differs from Cooking Lake by the greater number and irregularity of the lakes. Four separate basins occupied by muskegs were examined in this district.

No. 1 is a small area near Looma, not more than 200 yds. in diameter, similar in general topography to No. 1 previously described from the Cooking Lake district, but presenting more strongly marked features of retrogression.

The dominant plant is *Ledum groenlandicum*, but this is tending to die out, particularly in certain spots, as will be described later. Accompanying

plants in the order of their abundance are: *Eriophorum vaginatum* Torr., *Vaccinium canadense* Kalm., *Cladonia rangiferina* Web., *Vagnera trifolia* (L.) Morung, *Polytrichum commune* L., *Rubus chamaemorus* L., *Vaccinium vitis idaea* L. *Vaccinium oxycoccus* is only represented by occasional isolated plants and from the authors' knowledge of this muskeg the relative quantity of this plant seems to have decreased during the last five years. On the other hand, *Cladonia* is increasing and is invading both *Sphagnum* and *Polytrichum* patches.

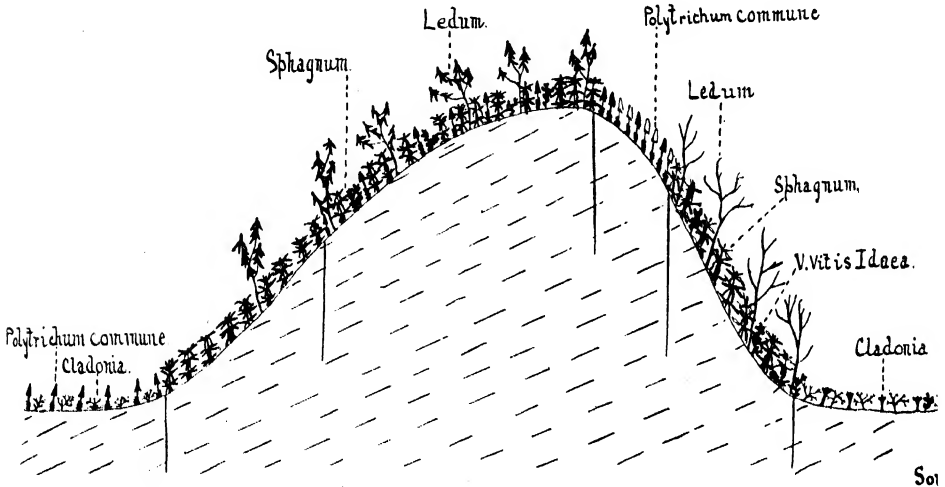


FIG. 2. *Sphagnum* mound, showing dying back of vegetation on S. facing slope. Vegetation in black is living, in outline dead. No. 1 Muskeg, Looma district.

The appearance of a mound in this muskeg is illustrated in Fig. 2. It shows that these mounds, which cover the surface, while built up by the original *Sphagnum* covering, are now being invaded by a different type of vegetation, particularly on the slopes facing the south. Because of this the appearance of the muskeg is entirely different according to whether it is viewed from the south or the north. Viewed from the north the mounds appear to be covered with a good growth of *Sphagnum* and *Ledum*. From the south they appear brownish in colour, being covered with dead *Polytrichum commune* and dead *Ledum*, only the lower slopes of the south face having a slight growth of *Sphagnum*. The depressions between the mounds are covered chiefly with *Cladonia rangiferina*. A border of *Carex* bog surrounds the muskeg, this being invaded at the outer edge by willow scrub.

In comparing the pH concentration of the waters from the marginal *Carex* bog and the muskeg itself there is found a steep gradient from salinity to a strongly acid reaction. The pH concentration of the water in the *Carex* bog is 7.5 and this remains constant to within 2 ft. of the edge of the muskeg. The water squeezed from the living *Sphagnum* on the north side of the mounds is pH 4.5.

No. 2. The general features of this small area are illustrated in Fig. 3. The surface of the muskeg is covered with mounds formed of *Sphagnum* peat but no living *Sphagnum* occurs except small isolated patches on the north face of a few of the mounds. The original flora appears to have been similar to No. 1 muskeg near Cooking Lake but progressive desiccation has caused an entirely different aspect. *Ledum groenlandicum* and *Sphagnum* were originally the dominant plants, but hardly a living plant is now to be found, although the surface is covered with dead branches. The living plants now consist of *Vaccinium canadense*, *V. vitis idaea*, *V. oxycoccus* (very rare), *Cladonia rangiferina* (scarce) and *Polytrichum commune*. This feature of retrogression is probably due to the exceedingly small size of this muskeg, the actual diameter being 200 ft.

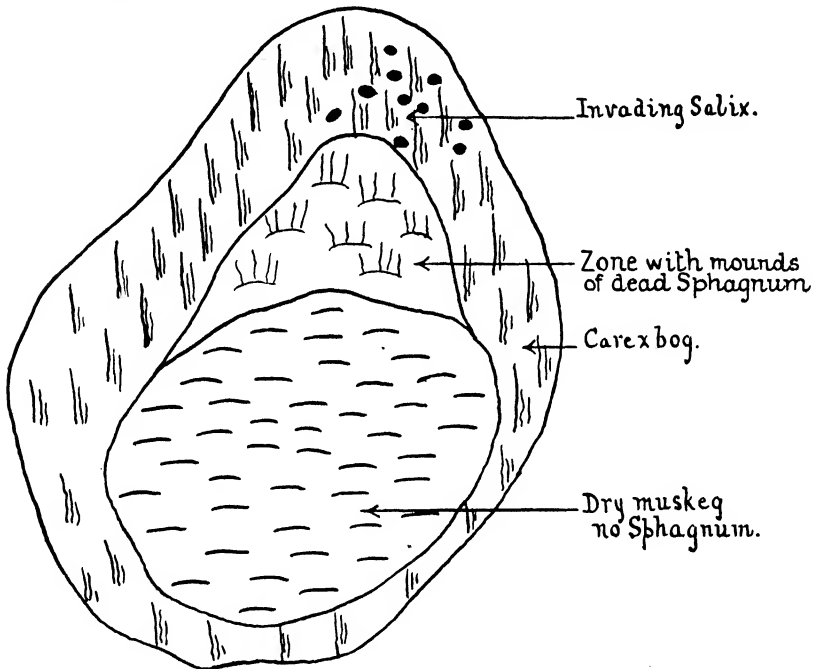


FIG. 3. Topographic sketch of No. 2 Muskeg, Looma district.

The *Carex* border averages about 30 ft. in width and in some places is being invaded by *Salix*. Between the north side of the muskeg and the *Carex* bog lies an intermediate zone showing mounds of *Sphagnum* peat, dead and much disintegrated and isolated patches of dead *Ledum*. The only living vegetation are plants which have immigrated from the surrounding poplar parkland. A complete list is as follows: *Epilobium angustifolium* Roth., *Lonicera involucrata* (Richards) Banks, *Equisetum sylvaticum* L., *Rubus arcticus* L., *Cornus canadensis* L., *Tussilago farfara* L., *Ribes* sp., *Salix* spp., *Populus tremuloides* (seedlings), *Carex canescens* L., *Calamagrostis canadensis* (Michx.) Beauv.

No. 3 is an example of extreme retrogression, the original muskeg having completely disappeared. The basin was originally even smaller than the one just described and the last vestige is now represented by small patches with isolated plants of *Ledum* and *Vaccinium vitis idaea*. On the small mounds (originally tenanted by *Sphagnum*) are now to be found many grasses, *Epilobium angustifolium*, *Equisetum sylvaticum*, and in the hollows between the mounds are *Rubus arcticus*, *Ribes* spp., *Potentilla comarum*, *P. monspeliensis*.

The pH of the water between the mounds was 6.0.

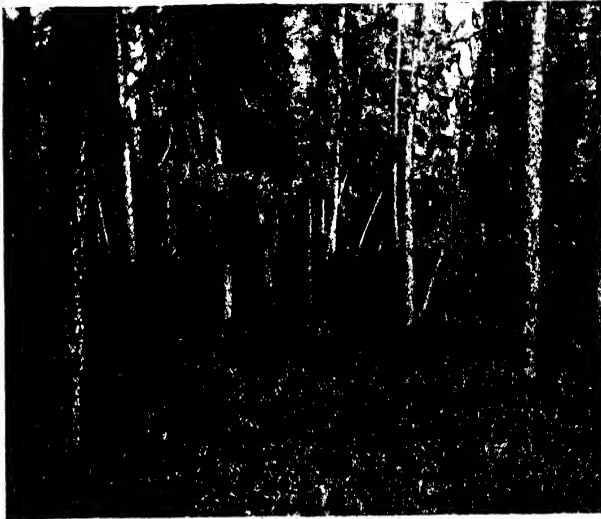
Other small peat areas in this district showed similar features; generally speaking the greatest evidence of retrogression due to desiccation is seen in the smaller muskegs.

THE STONY PLAIN MUSKEG

Large areas of the country to the west of Edmonton consist of muskeg. The region that has been particularly studied lies on the north side of the Saskatchewan River within a thirty mile radius of Edmonton. The long stretches of muskeg country in this district contrast sharply with the small isolated basins that are so plentiful to the east.

Passing westward from Winterburn (see Map) the main road rises over a lobe of plateau land at the 2300 ft. level covered with morainic deposits, and at Spruce Grove skirts the southern edge of the Sturgeon Valley which is marked out on the map by stippling—light between 2300 ft. and 2200 ft. and dark below 2200 ft., where there is an interrupted strip of muskeg in some places and fairly large white spruce in others growing on old muskeg ground. Our field observations show that during the retreat of the ice-sheet this part of the Sturgeon Valley was occupied by a lake, which at first was held up to the 2300 ft. contour line by an ice-lobe which filled the lower part of the valley of which Big Lake is now the centre. During this period the ice in the lower part of the valley dammed the outlet, and the head of the valley north of Stony Plain became filled with a marginal lake in which was deposited fine glacial silt, laid down as a marginal deposit below the 2300 ft. level. Subsequently, as the ice retreated, the valley became partly drained through the gorge now extending from St Albert to Sunny Glyde, Big Lake still remaining as the last remnant of this post-glacial lake.

The muskegs here, in spite of evident signs of retrogression, have not suffered so much from desiccation as those in the east, and this feature may be due to their larger size. They usually have a thick stand of *Picea mariana*, *Larix laricina* and *Betula papyrifera*, thus approaching more closely to the climax type. This is particularly noticeable at the margin, where they are usually bordered with a fringe of taller trees, so that from a height of land one may see, over the lower country in the distance, long stretches of muskeg covered by small trees, with a border of tall black spruce that stands out against the horizon.



Phot. 4. Forest of *Picea mariana* with *Ledum groenlandicum* at the west end of the Stony Plain muskeg (p. 327).



Phot. 5. West end of Stony Plain muskeg. Muskeg on the right, with *Picea mariana*, *Ledum* and *Sphagnum*. *Scirpus* bog on the left (p. 327).

An area about three-quarters of a mile long and one-third of a mile wide at the south-western edge of this post-glacial lake shelf has been studied in detail, and retrogressive changes of great interest due to the inflow of springs highly charged with mineral salts will be described. The muskeg is bounded on each of the three sides by rising ground, tenanted by large trees of *Picea albertiana* S. Brown coming from the parkland vegetation. A study of many of these borders seems to show that this tree flourishes particularly well on the decomposed peat of the margin of receding muskegs if the margin is well drained. The outstanding feature of this area is a lake (Plate VIII, Photos. 6-8), which, instead of representing a stage of upbuilding of the muskeg, is clearly encroaching upon it.

A plan of the general appearance of the area is shown in Fig. 4. The features presented by the numerous island outliers of mature tree-clad muskeg at the west end of the lake, and the character of the muskeg banks of the lake, at once suggested that the lake represented a stage of retrogression. It was not, however, until hydrogen ion concentration measurements of the lake and muskeg water were taken, borings over the lake bed and muskeg were carried out, and the dying back of *Sphagnum* near the lake and the presence of calcium salts in the peat noted, that this view became conclusive.

An account may first be given of the vegetation units of muskeg and *Carex-Scirpus* bog.

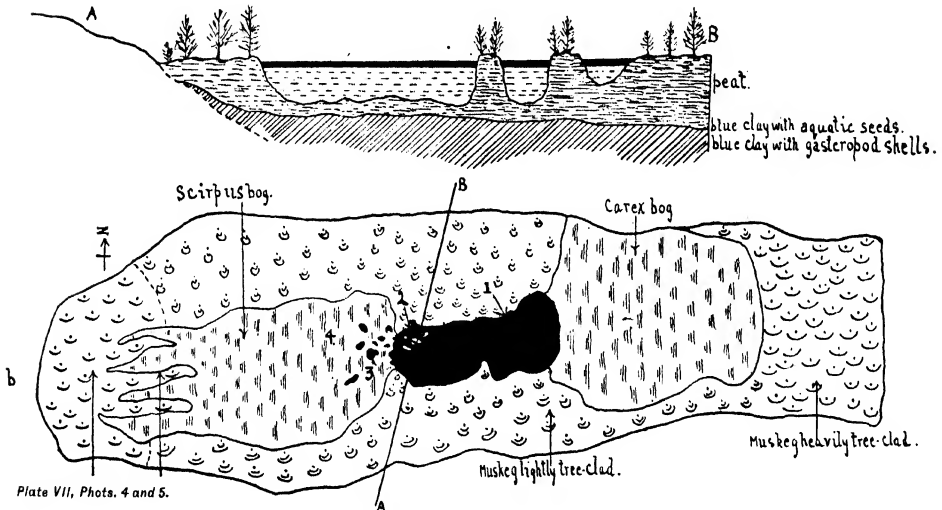


FIG. 4. Muskeg near Stony Plain. (a) Section along line A, B in plan, (b) showing calcareous lake occupying basin of decomposed peat with islands of peat still surviving. The numbers 1-4 indicate spots from which the water has been analysed (see p. 333).

THE MUSKEG AREA.

The dominant tree is *Picea mariana* (Mill) B.S.P. associated with *Larix laricina* and *Betula papyrifera*. The western and eastern ends are more heavily

tree clad (Fig. 4) and the muskeg is less denuded and more closely covered with vegetation. This is illustrated by Pl. VII, Phot. 4 and Pl. IX, Phot. 9.

The ground vegetation is composed of the following typical peat-forming plants which are here arranged in order of their relative abundance: *Ledum groenlandicum* Oedr., *Sphagnum acutifolium*, *Empetrum nigrum* L., *Hypnum* spp., *Vaccinium oxycoccus* L., *V. vitis idaea* L., *Drosera rotundifolia* L., *D. linearis* Goldie, *Rubus chamaemorus* L., *R. arcticus* L., *Vagnera longifolia* L. (Morung). With these plants, and particularly under the trees or near the margin of the lake, occur *Pyrola uliginosa*, *Orchis rotundifolia* Pursh, *Corallo-rhiza wisteriana* Conrad. On the more lightly wooded parts of the muskeg occur plants which suggest retrogressive changes, such as *Salix candida*, *Lonicera involucrata*, *Epilobium angustifolium* L., *Limnorchis dilatata* (Pursh) Ryd., *Cladonia rangiferina*, the latter being more abundant where the trees thin out.

Throughout the muskeg there are clear signs that retrogression is taking place, for the *Sphagnum* forming the familiar mounds on our muskegs is frequently dead towards the base, or in patches on the sides of the mound, and these are invaded by blue-green algae. When decomposition has proceeded for some time such dead patches become replaced by *Hypnum*, and it is not uncommon to see a partly decomposed *Sphagnum* mound made up of smooth patches of peat covered with blue-green algae, while other patches show a close sward of *Hypnum*. Tests carried out in the field showed a strong reaction for carbonates with dilute hydrochloric acid, a reaction not given when the reagent is used on the living *Sphagnum*.

The islands in the lake (Pl. VIII, Phot. 8) have essentially the same flora, save that *Sphagnum* is replaced to a great extent by *Hypnum*. This type of vegetation changes very little until the edge of the lake is approached when species of *Scirpus* and *Carex* with *Elephantella groenlandica* (Retz.) Ryd., *Parnassia palustris* L., *P. glutinosa* Pers., *Lonicera involucrata*, *Triglochim maritimum* L., form a narrow irregular fringe about 18 in. wide (Pl. VIII, Phot. 7).

It was not found possible to cut sections through the peat on account of the amount of water coming through, but borings with a 2 in. clay auger and 25 ft. extension rods were carried out in several spots of the muskeg, both within a few yards of the lake and near the margin of the area. All these borings agreed in showing a depth of 13 ft. underlain by stiff blue clay. *Sphagnum* appeared to be abundant in the peat to within a few inches of the bottom and the auger passed through the remains of tree trunks to within a few inches of the base of the peat. A thin layer at the base of the peat contains no *Sphagnum* and is made up of the remains of *Scirpus*.

The blue clay was bored through to a depth of 4 ft. or 5 ft. in various sections. It appeared to be uniform in character, containing very little water, with numerous quartz grains, generally less than 1 mm. in diameter. It quickly dries into a hard substance only fractured with difficulty. The upper



Phot. 6. Calcareous lake on the Stony Plain muskeg (cf. Fig. 4, p. 327).



Phot. 7. Stony Plain muskeg. Border of *Carex* and *Scirpus* on the lake bank (p. 328).



Phot. 8. Muskeg islands in the lake on the Stony Plain muskeg (p. 328).

layers contain numerous seeds or fruits of the following plants: *Hippuris vulgaris* L., *Potamogeton obtusifolius* Mert and Koch, *Potamogeton* sp., *Cyperus* sp., *Scirpus subterminalis* Torr. The remains of these aquatic plants appear to be confined to the upper 3 or 4 in. of the clay, at lower depths the very small shells of gastropods are exceedingly abundant to a depth of 4 to 5 ft. This gave a total depth (peat and clay) of 18 ft. from the surface, and was as far as it was possible for the boring equipment to penetrate owing to the exceeding stiffness of the clay. Mr J. A. Kelso, Director of the Industrial Laboratories, kindly had an analysis made of this clay, the result of which is given below.

Silica	62.2 %
Alumina	10.1
Iron oxide	3.1
Lime	7.6
Magnesia	1.4
Sulphates	nil
Phosphates (P_2O_5)	0.1
Ignition loss	14.4
Alkalies, etc.	1.1

Dr J. A. Allan, Professor of Geology, to whom we are indebted for an examination of the clay, reports that the material is a pure glacial silty clay deposited near the retreating ice-point. A similar clay occurs in the small basins between morainic ridges and mounds in the Cooking Lake and Looma districts and it is upon this impervious stiff glacial clay that all the peat deposits appear to rest, a matter of some interest, since it gives evidence that the peat bogs here described began to grow immediately after the last ice-sheet retreated from this country. This clay will be referred to later when dealing with the post-glacial history of this region.

CAREX AND SCIRPUS BOG.

Reference to Fig. 4 will show this extending as two irregular areas from the east and west end of the lake. At the west end the *Scirpus* runs into the muskeg as a series of winding channels, the boundary between these and the muskeg being exceedingly sharp as is shown in Pl. VII, Phot. 5. The muskeg dominated by *Ledum* and *Sphagnum* is seen on the right, the boundary resembling the bank of a stream formed of *Sphagnum*, the depressed *Scirpus* bog representing the stream.

The vegetation of the east end of the bog consists of *Carex aquatilis* Wahl., *C. stricta* Lam., *C. prairea* Dewey, *Eleocharis palustris* (L.) R. and S., *Juncus stygius* L., *Scirpus caespitosus* L., *Calamagrostis confinis* (Willd.) Nutt., *Cornus canadensis* L., *Tofieldia glutinosa* Pers. During the earlier part of the summer the water lies to a depth of 3 or 4 in. between the tufts of vegetation and becomes filled with a growth of *Utricularia intermedia* Hayne. Amongst this *Carex* bog occur mounds of muskeg vegetation varying in size from a few inches to a few feet across and rising about 6 in. above the level of the bog. These last traces of the muskeg vegetation amongst the *Carex* show various phases of retrogression from stages where there is still much *Sphagnum*

and where *Ledum* is the dominant plant, to others where the *Sphagnum* has been entirely replaced by *Hypnum* and the *Ledum* partly by species of *Salix*, whilst *Elephantella groenlandica* (Retz.) Ryd., is invading the margin of the mound. Small trees, some dead and others barely living, frequently cap the summits of these little mounds. The area of *Scirpus* bog west of the lake, particularly the long strips which run into the muskeg (Fig. 4, also Pl. VII, Phot. 5) frequently bear both larch and spruce, either singly or in patches; such trees are always stunted, partly defoliated or dead. They, like the muskeg mounds, must be regarded as part of the relict flora of the muskeg which formerly extended over these areas.

At the west end of the lake the vegetation is characterised by the following, in order of abundance: *Scirpus caespitosus* L., *S. pauciflorus* Lightf., *Juncus stygius* L., *Eleocharis acuminata* (Muhl) Nees, *Calamagrostis confinis*, *Carex aquatilis* Wahl., *C. stricta* Lam., *C. prairea* Dewey, *C. aurea* Nutt., *Triglochin palustre* L., *Tofieldia palustris* Huds., *Galium tinctorum*, *Limnorchis dilatata* (Pursh) Ryd.

Much of the valley bears a vegetation which is so much afloat that care has to be taken in walking over it not to break through. Borings were taken over this area both at the eastern and western end of the lake. All of them showed 13-15 ft. of peat which (below the surface liquid peat) contains abundance of *Sphagnum* down to the base, which rests on the same blue clay crowded with gastropod shells. There is then clear proof that the *Carex* and *Scirpus* bog at each end of the lake is a later invasion of these areas—originally muskeg—by the type of vegetation dominated by sedges, rushes and grasses, with other monocotyledons.

In the next section of this paper the degree of alkalinity or acidity of the water in the muskeg, in the *Carex* and *Scirpus* areas and in the lake are recorded (p. 333); the results of the analyses of samples of lake water are tabulated (p. 333); and the rate of tree growth on the muskegs is graphed (pp. 339-40).

THE LAKE AND DRAINAGE WATERS.

Seen during the summer, the waters of the lake are clear to a depth of about 6 in.; below this the water is filled with a greyish to pink deposit and this extends to a depth of about 9 ft. The muskeg banks, which are about 1 ft. above the water, go down abruptly, but during the summer it was not possible to investigate the lake or to reach any of the islands. During November, December and January the whole area is frozen and the lake covered with 2 ft. of ice, and it was during this period that borings were taken over the whole area through holes cut in the ice.

All the borings agree in showing that peat underlies the whole lake. The floor is uneven, but the average depth at which the peat is reached below the surface of the lake is 8-9½ ft. The depth from the surface of the lake to the

underlying blue clay (which is of exactly the same character as that underlying the adjacent muskeg, *Scirpus*, and *Carex* bog) is 13 ft. The lake then rests upon peat of an average thickness of $4\frac{1}{2}$ ft.; this is composed very largely of *Sphagnum* and is therefore an extension of the lower layers of the surrounding muskeg under the lake.

Great interest attaches to the borings taken on the small muskeg islands so numerous at the west end of the lake. In all cases *Sphagnum* peat extended down continuously from the surface to within a few inches of the clay floor 13 ft. below. These islands may be described as pillars of peat standing in the lake.

The spongy deposit filling up the lake to within about 6 in. of the surface is a peculiar algal colony which has attained the depth of about 8 ft., where it overlies the peat. Over its surface is spread a crust made up of pink flakes a few inches in diameter, curled up at the edges to reveal a blue-green under surface. This surface layer is richer in blue-green algae than is the rest of the deposit. When this is skimmed off there is exposed a pink substratum smelling strongly of hydrogen sulphide. It is made up of soft nodules forming a porridgy mass which can be stirred up with a stick. In it is embedded a large quantity of *Chara*, and near the border *Utricularia* is abundant. As is shown below, it is particularly rich in diatoms and unicellular green algae.

Various collections of this material were made and brought back to the laboratory for examination. It soon became evident that the deposit was an extremely rich algal growth. Material collected during September and October was sent to Mr C. W. Lowe, M.Sc., of the University of Manitoba, who kindly consented to examine it and we are much indebted to him for the following extensive list of algae from this deposit.

Collection No. 1 was taken from the crust already mentioned overlying the deposit, collections No. 2, 3 and 4 from the deposit itself. No. 2 was from the west end of the lake in September; No. 3 from near the centre during November; No. 4 from a smaller lake on the *Scirpus* bog. Nos. 5 and 6 are from submerged vegetation along the margin, the former growing on *Hypnum*, the latter on *Utricularia*. Sample No. 7 contained a mass of a fresh-water sponge, either *Spongilla fragilis* or *Spongilla lacustris*.

LIST OF ALGAE.

<i>Myzophyceae</i>				1	2	3	4	5	6
<i>Chroococcus turgidus</i> (Kütz.) Näg.	+	.	+	.	.	+
<i>C. limneticus</i> Lemm.	+
<i>C. macrococcus</i> (Kütz.) Raben.	+
<i>Gloeocapsa fusco-lutea</i> (Näg.) Kütz.	+
<i>Aphanothece saxicola</i> Näg.	+
<i>Microcystis</i> sp.	+
<i>Gomphosphaeria aponina</i> Kütz.	+	.	.	.	+	+
<i>Coelosphaerium kützingianum</i> Näg.	+	.	+	.	+	+
<i>Merismopedium tenuissimum</i> Lemm.	+	.	+	.	+	.
<i>Lyngbya aerugineo-caerulea</i> (Kütz.) Gomont.	+	.
<i>Stigonema minutum</i> (Ag.) Hass.	+
Also fragments of <i>Oscillatoria</i> , <i>Rivularia</i> , <i>Nostoc</i> and <i>Anabaena</i>				+	.	.	.	+	+

LIST OF ALGAE (continued).

<i>Bacillariaceae</i>	1	2	3	4	5	6
<i>Amphora ovalis</i> Kütz.	+	.	+	.	+	.
<i>Cymbella cymbiformis</i> Ehr.	+	.	.	+	+
<i>C. cymbiforma parva</i> (W.Sm.) H.V.H.	+	.	.	.
<i>C. gastroides</i> Kütz. forma minor H.V.H.	+	.	.
<i>C. ehrenbergii</i> Kütz.	+	.	+	.	.	.
<i>C. lanceolata</i> Ehr.	+	.	+	.	.	.
<i>Stauroneis phoenicenteron</i> Ehr.	+	+
<i>Navicula viridis</i> Kütz.	+	.	+	.	+	.
<i>N. oblonga</i> Kütz.	+	.	+	.	.	+
<i>N. radiosa</i> Kütz.	+	.	.	.
<i>N. radiosa</i> var. <i>acuta</i> (W.Sm.) H.V.H.
<i>N. cuspidata</i> Kütz.	+	.	.	.
<i>N. sphaerophora</i> Kütz.	+	.	+	.	.	.
<i>N. iridis</i> Ehr.	+	.	.
<i>N. iridis</i> var. <i>producta</i> H.V.H.	+	+	.	.
<i>Gomphonema constrictum</i> Ehr.	+	.	.	+
<i>G. intricatum</i> Kütz.	+	.	+	.	.	.
<i>Epithemia turgida</i> (Ehr.) Kütz.	+	.	+	.	.	+
<i>E. argus</i> Kütz.	+	.	+	.	.	+
<i>Rhopalodia gibba</i> (Kütz.) O. Müll.	+	.	+	.	.	+
<i>Synedra ulna</i> (Nitzsch.) Ehr.	+	.	+	.	.	.
<i>S. ulna</i> var. <i>splendens</i> (Kütz.) H.V.H.	+	+
<i>Fragilaria crotonensis</i> (A.M.Edw.) Kitton	+	.	.	.
<i>F. capucina</i> Desmaz.	+
<i>Surirella</i> sp?	+	.	.	.
<i>Hantzschia amphioxys</i> (Ehr.) Grun.	+	.	.	+
<i>H. amphioxys</i> var. <i>elongata</i> H.V.H.	+	.	+	.	+	.
<i>Chlorophyceae</i>						
<i>Oocystis solitaria</i> Wittr.	+
<i>Tetradron minimum</i> (A.Br.) Hangs.	+	.
<i>Scenedesmus quadricauda</i> (Turp.) Bréb.	+	+	+	+	+
<i>Coelastrum microporum</i> Näg.	+
<i>Pediastrum tetras</i> (Ehr.) Ralfs	+	.	+	.
<i>P. boryanum</i> (Turp.) Menegh.	+	.	.	+	+	.
<i>Cylindrocapsa conferta</i> W. West	+
<i>Spirogyra</i> (not in conjugation)	+
<i>Euastrum dubium</i> Näg.	+	.	+	.	.
<i>E. insulare</i> (Wittr.) Roy.	+
<i>Cosmarium granatum</i> Bréb.	+	+	+	+	+	+
<i>C. rectangulare</i> Grun.	+	+
<i>C. impressulum</i> Elfv.	+	+
<i>C. laeve</i> Raben.	+	.	.
<i>C. pokornyanum</i> (Grun.) W.W. and G.S.W.	+
<i>C. hammeri</i> Reinsch.	+
<i>C. quadrum</i> Lund.	+
<i>C. humile</i> (Gay) Nordst. var. <i>striatum</i> (Boldt) Schm.	+	+
<i>C. subeucumis</i> Schm.	+
<i>C. reniforme</i> (Ralfs) Archer	+
<i>C. subcrenatum</i> Hantz.	+	.	.	+	+	.
<i>C. botrytis</i> (Bory) Menegh.	+	+
<i>C. margaritaceum</i> (Lund) Roy and Bissett	+
<i>Staurastrum muticum</i> Bréb.	+	+
<i>S. polymorphum</i> Bréb.	+	.	.
<i>S. alternans</i> Bréb.	+
<i>S. paradoxum</i> Meyen	+	+
<i>Parbochaete</i> sp? (Not in fruit)	+	.	.	.
<i>Ophioctytium cochleare</i> (Eichw.) A.Br.	+

Chara is also an important member of this lake flora. It occurs at the surface of the lake, particularly at the western end, in considerable abundance and is met with living in the upper layers of the calcareous deposit in the lake. Its remains can be recognised amongst the calcareous deposit at much greater

depths. Mr James Groves has kindly examined the material and has informed us that the species is *Chara contraria* with numerous root bulbils—the first instance of root bulbils found in this species.

REACTION AND ANALYSIS OF WATER.

We have, then, a calcareous lake with clear surface water and 9 ft. of calcareous material below resting on a floor of peat bounded by banks of peat.

There being no stream either flowing into or out of this lake the level must be maintained by underground springs, which, as the evaporation from the surface during the hot summer months is considerable, and as the level does not noticeably vary, must be of just sufficient flow to replace evaporation.

The acidity or alkalinity of the waters of the lake, the water on the surface of the *Carex* bog, and the water held in the masses of *Sphagnum* on the muskeg area have been measured in the field by means of pH indicators, the values so obtained being as follows:

Muskeg area.	Water squeezed from living <i>Sphagnum</i>	pH	4.5
<i>Carex</i> bog.	Water from surface between tufts of vegetation	pH	7.5
Lake.	Water from surface layers	pH	9

That the lake water with a pH value as high as 9 should be bounded by banks of peat with *Sphagnum* having a pH of 4.5 shows quite clearly—even without the observations concerning the substratum—that the lake must represent a retrogressive rather than a progressive stage in the history of this muskeg region.

Certain indications point to the western end of the area as the place of outlet of the springs feeding the lake. The *Scirpus* bog at the western end is more obviously afloat than the *Carex* bog at the eastern end, while at the same time the eastern end is somewhat firmer but bears more water on the surface.

In order to see whether there is any marked difference in the water from different regions, samples have been taken from four different spots which are marked 1, 2, 3, 4 respectively in Fig. 4. No. 1 sample was taken from the surface water about 2 ft. from the bank, No. 2, 3 ft. from the bank of a small bay. No. 3 from one of the numerous small pools which break the surface of the floating *Scirpus* bog. No. 4 was obtained by cutting away the floating mat of *Scirpus* and obtaining the sample from below. The analyses of these samples were carried out by the Provincial Industrial Laboratories and the results are as follows:

Parts per Million.

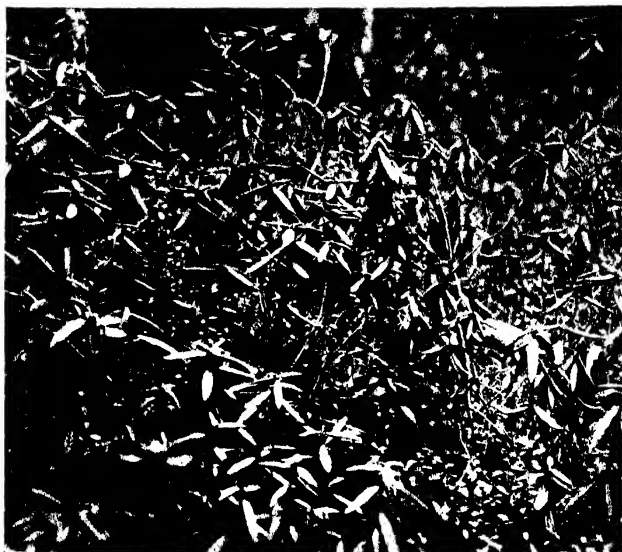
	No. 1	No. 2	No. 3	No. 4
Calcium	53.0	61.8	78.2	86.1
Magnesium	25.8	29.6	41.2	39.2
Sodium	4.0	6.5	5.2	9.6
Sulphates (SO ₄)	53.9	61.8	44.2	60.0
Carbonates (CO ₃)	102.3	103.9	185.7	181.1
Silica	0.4	0.2	0.4	0.4
Iron Oxide and Alumina	nil	nil	nil	nil
Vegetable Matter	99.0	82.0	42.3	58.0
Total Solids	355.3	383.6	413.9	461.0

The progressive increase of mineral salts in solution, particularly of calcium carbonate and magnesium carbonate, as one passes from the east end of the lake to the *Scirpus* bog at the western end suggests that the springs feeding the lake have their outlet in the western region of the area and this is borne out by the curious winding channels of *Scirpus* bog which intersect the muskeg in this region.

The tests of the H-ion concentrations and the collection of water samples were made in the autumn before the area became frozen. Measurements of the rate of growth of trees from this and other muskegs have been carried out and these are described in a later section of this paper.

It seems clear from the features described here that the muskeg began its history during the retreat of the ice-lobe from the Sturgeon basin. The nature of the clay and the presence of gastropods indicate the presence of an early post-glacial lake, the seeds and fruits of aquatic plants in the upper layers representing the primary free-floating vegetation of this lake. By the action of the overflow stream cutting through the glacial deposits blocking the trench between St Albert and Sunny Glyde (see Map), the level of the lake became progressively lowered, leaving the border of fine clay exposed, and upon this a vegetation composed of sedges and rushes succeeded the free-floating vegetation of the former lake. Not very much peat appeared to be formed by the *Carex* bog, but when *Sphagnum* and accompanying peat-forming plants spread, the subsequent growth of the muskeg must have been continuous until about 12-13 ft. of peat was formed—probably representing, in this northern climate with a short growing season, a considerable length of time. At length springs rich in calcium sulphate, calcium carbonate and magnesium carbonate broke out where the lake now stands. Springs as rich in calcium and magnesium salts as the water analyses show would certainly stop the further growth of *Sphagnum* and other peat-forming plants. As a result the bare peat would be exposed and water from the springs would collect in hollows on the surface of the peat bog. The exposure of a bare peat surface, the presence of organisms setting up decomposition in the peat, and mineral salts in considerable concentration, might be expected to produce in time a basin, which, owing to the causes mentioned, would tend to widen and deepen. The algae and *Chara* present in such enormous abundance are the chief agents responsible for the great precipitation of mineral salts above the floor of the lake.

Such curious retrogressive changes in peat deposits are not in the authors' experience common, although the breaking out of springs richly charged with mineral salts is not uncommon, particularly in the country west of Edmonton. In a ravine coming into the Saskatchewan Valley a few miles west of Edmonton springs have formed a tufa deposit of considerable thickness and the decomposition of an adjacent small peat bog may be due to the percolation from such springs. Another peat deposit a few miles north of Stony Plain



PHOT. 9. *Ledum groenlandicum* and *Empetrum nigrum*.
West end of Stony Plain muskeg.



PHOT. 10. Muskeg surrounded by ground cleared of poplar woodland and now
planted with oats. Dec. 1925 (see p. 335).

near Calahoo, on the same line of muskeg country, exhibits a somewhat similar feature, although owing to the thinness of the peat deposit only a shallow basin has been formed, the floor of which is covered with calcareous marl. Owing to the area occurring on a slope, the hollow is not permanently filled with water and the algal deposit is therefore dried up except during the early part of the summer. These other cases have not been investigated in detail, and are only quoted here as a suggestion that the features recorded may not be uncommon on muskegs situated on the Edmonton geological horizon.

RETROGRESSION DUE TO CLIMATIC FACTORS AND FIRE

Peat bogs in the parkland belt generally show distinct stages in retrogression, and the type of vegetation is now markedly different from the abundance of *Sphagnum* that must have characterised these areas at the period of their maximum growth. In the southern region of the parkland and Edmonton district the muskegs tend to be confined to small basins frequently only a few hundred yards or less in diameter, and stand as islands of peat bog vegetation in the surrounding poplar woodland. Large continuous areas of peat are not usually met with until the northern coniferous forest is reached. Generally speaking the evidences for retrogression are more marked in the south although the actual size of the basin is obviously a contributing factor. An average annual precipitation varying from 12 in. to 22 in. and a growing season of only four months in the year are not conditions which might be expected to favour the formation of extensive peat deposits. Evidences of the curiously localised condition of these peat areas and the abrupt changes of vegetation at their margin are frequent, and an interesting example is shown in Pl. IX, Phot. 10. Here the muskeg originally lay as a narrow winding strip in poplar woodland. The woodland has been cleared and the ground (black soil) cultivated. The photograph shows the stubble of an oatfield passing up to the edge of the narrow fringing *Carex* surrounding the muskeg. Living *Sphagnum* may be absent on such a peat bog at the present time although the peat below is formed very largely of this moss.

The origin of the muskegs must be sought in small lakes which dotted the morainic areas of the parkland after the recession of the ice, the flora of the lakes being represented by the seeds and fruits of aquatic plants from the surface of the blue clay underlying some of the areas described in this paper. From that period to the stage when the muskegs began to show retrogression, their history appears to be one of uninterrupted upbuilding by *Sphagnum*, and small trees of black spruce and larch seem to have been present throughout this stage. How long the retrogression period has lasted and how far the stages have been accelerated by fire and later by man's influence we have at present no evidence to show. The retrogression stages are probably slow compared with those which might take place in a country

with an open winter such as north-western Europe, for in this region the surface is usually frozen for seven months in the year.

The dying back of *Sphagnum* seen on the south facing slopes of the mounds on some muskegs appears to suggest decreased precipitation and increased evaporation. It is possible that this may be due in part to the immense amount of clearing and draining that has taken place in the parkland belt during the last 40 years. The effect of settlement has been to clear off as much of the natural vegetation cover as possible in order to obtain areas for cultivation and the making of roads and cutting of drains has resulted in a great reduction of surface waters. This is all to the good up to a certain point, since clearing, draining and cultivation undoubtedly reduce the chance of late and early frosts which are a menace to successful cultivation. But in a country with a moderate rainfall and a very high rate of evaporation during the summer months, it may be doubted whether the indiscriminate draining of lakes and all reserves of surface waters is advisable. Many of the larger lakes in the Edmonton district such as Beaver Lake are quite shallow, being not more than 14 ft. in depth. The draining of such lakes is frequently discussed and could be effected without serious difficulty, but such a policy, if completely carried out, would certainly tend to increase aridity.

Another factor that must be considered in regard to retrogression is fire. In a country in which forest fires have been so frequent in the past, it might be expected that very few of the muskegs would have escaped burning over. This may be the case, but on the other hand numerous examples occur like that shown in Pl. X, Phot. 12, where the muskegs are closely covered with symmetrical trees of black spruce. These may be small but growth is slow and such trees are usually about 50 or 60 years old. In a season dry enough to permit burning, spruce in which the branches come to the ground would be highly inflammable, and if not destroyed would certainly retain the marks of burning. There are other muskegs which have clearly been burnt over, an interesting example of this being illustrated in Pl. X, Phot. 11. This little muskeg in the Cooking Lake district is almost circular and not more than 200 ft. in diameter. Remains of burnt black spruce still occur on the surface but the only trees growing at present are birch and poplar which have spread in from the surrounding parkland. No *Sphagnum* occurs and the original muskeg flora is largely replaced by grasses, willows, lichens, and *Vaccinium vitis idaea*. It is difficult to estimate the length of time since burning, but the birches average about 30 years of age and the burning was severe enough to char the surface of the peat, the signs still remaining.

Other cases occur in which the peat has been destroyed to a considerable depth, but this seldom extends over the whole muskeg and frequently mounds and banks occur in areas which were too wet for the fire to enter and where the original muskeg flora still remains but little changed. In some cases where a muskeg area adjoins cleared cultivated land, intentional burning



Phot. 11. Birch and poplar invading a burnt-over muskeg near Cooking Lake. Original vegetation nearly destroyed (p. 336).



Phot. 12. *Lediton groenlandicum* and *Picea mariana* on muskeg in the Cooking Lake district (pp. 322-3).

is carried out and this may proceed for several years and be so thorough as to expose the underlying clay.

The several muskeg areas lying upon the blue glacial clay date back to the period immediately following the recession of the ice-sheet. Fires were more frequent and widespread before the coming of the white man than they are at present as they are now carefully controlled. It must be concluded that if burning was a frequent factor in retrogression the muskegs would not have acquired their present depth of peat. Further, in examples examined by one of us several years ago by means of sections, thin charred layers of peat were present sometimes several feet (4-6 ft.) below the present surface and the peat above the charred layer was formed chiefly of *Sphagnum*. This suggests that at a former period a muskeg could entirely recover its original vegetation after burning; from examples of more recent burning this does not seem to be the case at the present day. The general conclusion we have been led to by our observations is that retrogression occurs to-day from desiccation caused by changed meteorological conditions and the general clearing and draining of the country and that burning, while locally important as producing marked retrogression and even complete destruction of the muskeg, is not responsible for the general shrinkage in growth and change of vegetation so marked in the whole area examined. Muskegs in the central and southern region of the parkland so near prairie must be looked on as relics of a former condition more favourable for peat formation.

THE AGE AND VARYING RATE OF GROWTH OF TREES ON MUSKEGS.

The correlation between the rate of growth of trees and the climatic factor has been a frequent subject of discussion in plant ecology and forestry for a number of years. The most detailed study hitherto made is that by A. E. Douglass¹ on *Sequoia*, Yellow Pine and other trees.

It having been ascertained by us that the trees, although small, are of considerable age, an examination of sections has been made with the object of measuring fluctuations in the rate of growth in former periods and of deciding whether there are any marked differences in muskegs of various types and stages.

With this object sections of trees were taken at a height of about 2 ft. from the ground and for each tree the number of mm. of wood added every ten years (this time period being selected as an arbitrary standard) were measured and recorded graphically. The records show an acceleration of growth in the first 25 years of the life of the tree, which disappears later. This is due not to any climatic factor but to the fact that trees have a higher rate of growth in youth than in maturity. The tree curves discussed here have

¹ A. E. Douglass. "Climatic Cycles and Tree Growth." Carnegie Inst. Wash. Publ. 289, 1919. See also Ellsworth Huntington. "The Climatic Factor as illustrated in arid America." Carn. Inst. Publ. 192, 1914.

been corrected for this factor according to the method described by Douglass by subtracting the average "Curve of Youth" from each one, and this results in a straightening out of the curve for the first 25 years.

About fifteen trees from the muskeg at Stony Plain were measured, the five shown in Fig. 5 being representative. These all show similar well-marked fluctuations for the last 105 years.

The graphs show two maximum periods of growth, one about 1835, and the other after 1905, while in 1885 there is a period of regression. Every tree without exception shows a maximum growth during 1835. The minimum period 1885 is becoming apparent in some of the trees 10 or 20 years before, but on the whole the agreement is remarkably uniform. All the trees increase their rate of growth after the year 1905 and in some cases after 1865, but during the last 10 years there is a lack of uniformity, for in about a third of the trees measured the growth fell off and in the remainder it increased.

In Cooking Lake Muskeg No. 2, in which the vegetation shows distinct signs of desiccation, trees have been examined which show the same curves as those from Stony Plain. The fluctuations in this muskeg are shown in Fig. 6. As these trees are younger and because the curve for the first 30 years (being partly due to youth) has been omitted, only a few trees go back to the maximum of 1835. The minimum growth period of 1895 and the maximum of the last 20 years correspond perfectly.

These results strongly suggest that in the last 100 years, there were two maximum periods of rainfall—one about 1835 and the other about 1915, and that the period of 1885 was one of drought.

The most remarkable feature shown in these records is the enormous increase in the rate of growth in the trees from Cooking Lake Muskeg No. 2, compared with those from Stony Plain:

Average rate, mm. per year, Cooking Lake, No. 2	1.13
" " " " Stony Plain	0.31

thus showing that the trees on the smaller well-drained muskeg with a more retrogressive type of vegetation are growing about four times as quickly as those on the muskeg which approximates more closely to a climax type.

It has also been observed that the trees of Stony Plain grow at a greater rate towards the east end where the *Sphagnum* is not growing so vigorously. Again, the largest trees are nearly always found along the receding border of the muskeg; as the muskeg has been tree-clad throughout its history, this is not due to invasion taking place from the margin but to an actual increase in growth rate.

The fact that the rate of growth of trees on a muskeg is the converse to the rate of growth of *Sphagnum* is borne out by G. B. Rigg¹ in a study of the growth of trees on the muskegs of the Pacific coast, where he observes that

¹ G. B. Rigg. *Bot. Gaz.* 65, 1918, p. 359.

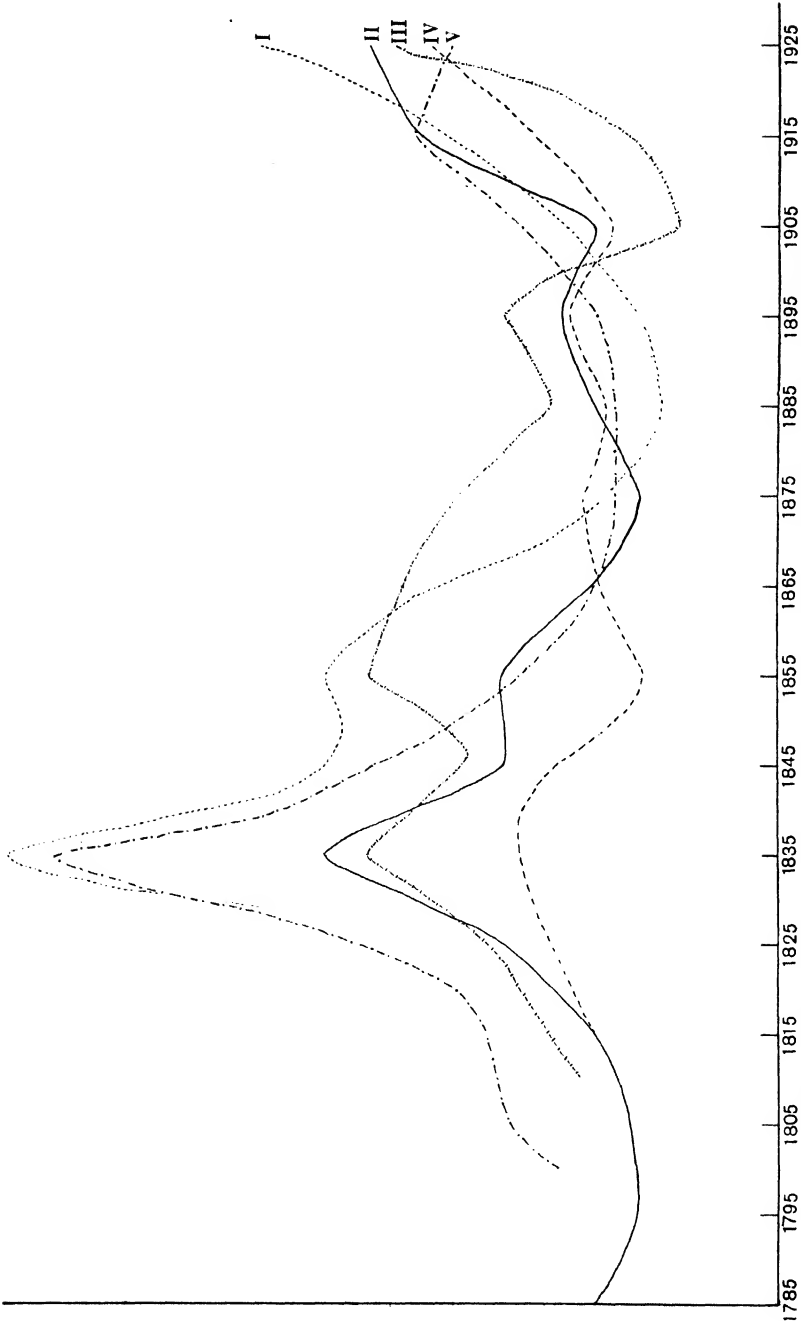


FIG. 5. Graphs showing 10-year increments of five representative trees from Stony Plain Muskeg.
The first parts of the graphs are corrected for youth (see text).

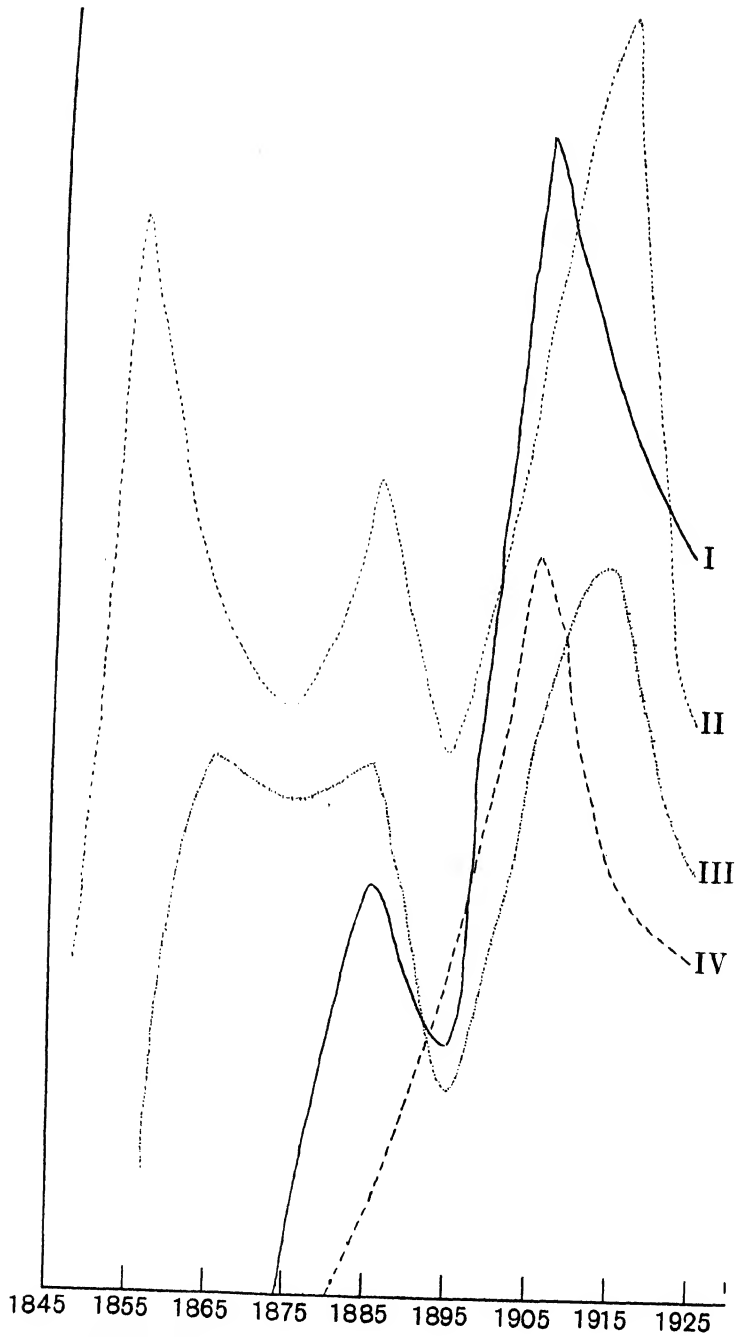


FIG. 6. Graphs of tree-growth from Cooking Lake Muskeg No. 2
(first 30 years of growth not included).

trees are retarded in growth when on actively growing muskegs owing to the toxic influence of the *Sphagnum*.

It would be expected in a muskeg of the type of Cooking Lake No. 2—small, rapidly receding and with *Sphagnum* scanty and in poor condition—that the acidifying effect of the moss would be at a minimum and the conditions for tree growth most favourable. In fact the pH of the Cooking Lake muskegs is 5 and Stony Plain *Sphagnum* is 4.5.

SUMMARY.

1. The vegetation, history and retrogressive changes of muskegs in the poplar parkland district of Edmonton are described.

2. *Sphagnum* is tending to disappear and to be replaced by vegetation indicating drier conditions and a cessation of peat-formation.

3. These muskegs are formed on fine glacial clay in small basins in morainic regions. Seeds of aquatic plants are present in the surface layers of the clay, which is covered with a few inches of *Scirpus* peat. *Sphagnum* has dominated the muskegs until more recent times.

4. Retrogressions due to fire, desiccation and the inflow of springs highly charged with mineral matter, causing the formation of a calcareous lake in a peat basin, are described.

THE SALT MARSH VEGETATION OF LITTLE ISLAND, Co. CORK

By R. H. McCREA, B.Sc.

(*With one Figure in the Text.*)

The following ecological study, with the exception of the chemical analyses, was made during a holiday in August, 1924.

Little Island is situated in the tidal part of the River Lee, roughly half-way between Cork and Queenstown. *Fucus* and *Enteromorpha* grow in abundance on its shores. It is at the present time not really an island but a peninsula, being joined to the mainland by more or less swampy meadows, through which drains are cut, and from which the high tides are excluded by means of dams and sluice-gates. It appears, from local information, that the date of reclamation can be fixed approximately at three-quarters of a century ago.

The "island" consisted at that time of four distinct islands, the intervening land between these having been reclaimed and preserved in much the same way. These reclaimed lands are shown as shaded regions in Fig. 1.

It is these features which lend special interest to the flora of the locality, as various stages in its development can be traced from the typical salt-marsh vegetation, which is frequent on parts of the unreclaimed shores, to that of the "artificial marsh-meadow" of Warming (4), which affords excellent grazing material for cattle and horses and an abundant yield of coarse hay.

Little Island is about three miles long by about one to one-and-a-half wide, and rises to some hundred feet towards the centre. The rock, which emerges in many places towards the south side, is a magnesian limestone. The whole is well planted with trees and the land is remarkably fertile.

I. CHLORIDE-CONTENT AND VEGETATION.

A slight attempt has been made to correlate the percentage of chlorides, estimated as sodium chloride, with the type of vegetation. Sir E. J. Russell (2) cites experiments which show that a slight amount of chloride is in some cases beneficial, but "beyond a relatively low concentration limit further increases in amount of sodium chloride proved toxic." Sodium does not appear to be essential even to salt-marsh plants, but A. C. Halket (1) found that *Salicornia* grew better in its presence.

The method employed for chloride estimation is that given by H. J. Page (3) of Rothamsted, where the extract from a known weight of soil is treated with a known volume of standard silver nitrate and the excess titrated with decinormal ammonium thiocyanate, using ferric sulphate as indicator.

The first sample of soil was taken outside the sea wall from a part of the beach flooded at high water; the remaining samples were taken inside the sea wall from parts of the reclaimed marsh at varying levels above the drainage water.

Percentage of sodium chloride in soil	Flora of Region	Frequency	Percentage of sodium chloride in soil	Flora of Region	Frequency
7.36	<i>Statice Limonium</i>	} Abundant	0.28	<i>Ranunculus repens</i>	} Very abundant
	<i>Spergularia rubra</i>			<i>Leontodon hispidus</i>	
	<i>Festuca rubra</i>			<i>Juncus communis</i>	} Frequent
2.31	<i>Triglochin maritimum</i>	} Very abundant		<i>J. obtusiflorus</i>	
	<i>Juncus obtusiflorus</i>			<i>Holcus lanatus</i>	
	<i>Agrostis alba</i>	Abundant		<i>Cynosurus cristatus</i>	} Occasional
	<i>Carex vulpina</i>	} Frequent		<i>Agrostis alba</i>	
	<i>Apium graveolens</i>			<i>Lotus corniculatus</i>	
	<i>Aster tripolium</i>			<i>Alopecurus pratensis</i>	
2.09	<i>Agrostis alba</i>	Very abundant	0.23	<i>Agrostis alba</i>	Very abundant
	<i>Juncus glaucus</i>	} Abundant		<i>Mentha arvensis</i>	} Frequent
	<i>Cirsium arvense</i>			<i>Ranunculus repens</i>	
	<i>Trifolium repens</i>	} Frequent		<i>Trifolium repens</i>	
	<i>Potentilla anserina</i>			<i>Cirsium arvense</i>	} Occasional
	<i>Carex vulpina</i>			<i>Festuca rubra</i>	
	<i>Festuca rubra</i>				

II. TRANSITION VEGETATION (RECLAIMED).

The reclaimed land marked *A* on the map (Fig. 1) contains a long drain from the higher reclaimed land *C*, and a somewhat large pool near its centre. This marsh is cut off from the sea by a long wall, banked up on the inner side

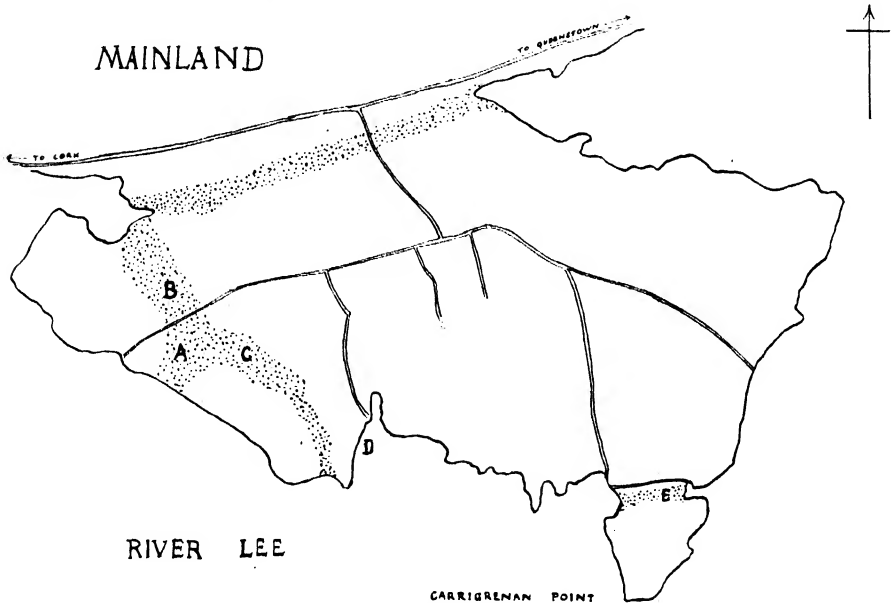


Fig. 1.

344 *The Salt Marsh Vegetation of Little Island, Co. Cork*

by dredgings from the river-channel, and it appears to be customary to run off the drainage-water once yearly. At high tide the greater part of this land, and also that marked *B*, is much below the level of the river outside. These two tracts which were originally one are now separated by an embanked road, and on the whole *B* is drier than *A*.

The method employed for tabulating this vegetation was to take quadrats in typical patches at regular distances apart with the view of noting the influence of increasing dryness of the soil on the flora.

QUADRATS IN <i>A</i>		QUADRATS IN <i>B</i>	
Wettest region.			
%		%	
40	<i>Triglochin maritimum</i>	40	<i>Juncus glaucus</i>
40	<i>Juncus obtusiflorus</i>	20	<i>Potentilla anserina</i>
10	<i>Agrostis alba</i>	10	<i>Trifolium repens</i>
5	<i>Carex vulpina</i>	10	<i>Lotus corniculatus</i>
5	{ <i>Apium graveolens</i>	5	<i>Holcus lanatus</i>
	{ <i>Aster tripolium</i>	5	<i>Ranunculus repens</i>
			{ Moss
			{ <i>Trifolium pratense</i>
		10	{ <i>Epilobium palustre</i>
			{ <i>Arenaria uliginosa</i>
			{ <i>Geranium dissectum</i>
			{ <i>Carex vulpina</i>
Drier region.			
65	<i>Agrostis alba</i>	30	<i>Holcus lanatus</i>
15	<i>Triglochin palustre</i>	20	<i>Ranunculus repens</i>
15	<i>Potentilla anserina</i>	10	<i>Juncus glaucus</i>
5	<i>P. erecta</i>	10	<i>Agrostis alba</i>
		10	Moss
		10	<i>Juncus bufonius</i>
			{ <i>Prunella vulgaris</i>
			{ <i>Carex axillaris</i>
		10	{ <i>Lotus corniculatus</i>
			{ <i>Potentilla tormentilla</i>
			{ <i>P. anserina</i>
			{ <i>Rumex nemorosus</i>
Drier still.			
30	<i>Agrostis alba</i>	30	<i>Ranunculus repens</i>
15	<i>Trifolium repens</i>	20	<i>Agrostis alba</i>
15	<i>Juncus glaucus</i>	15	<i>Rumex nemorosus</i>
15	<i>Cirsium arvense</i>	15	<i>Cirsium arvense</i>
10	<i>Carex axillaris</i>	5	<i>Juncus glaucus</i>
10	<i>Festuca rubra</i>	5	<i>Trifolium pratense</i>
5	{ <i>Ranunculus repens</i>	5	<i>Holcus lanatus</i>
	{ <i>Vicia sepium</i>	5	<i>Prunella vulgaris</i>
			{ <i>Rumex acetosa</i>
		5	{ <i>Plantago major</i>
			{ <i>Potentilla anserina</i>
			{ <i>Lotus corniculatus</i>
Driest region.			
60	<i>Agrostis alba</i>	70	<i>Agrostis alba</i>
15	<i>Mentha arvensis</i>	15	<i>Rubus fruticosus</i>
10	<i>Ranunculus repens</i>	5	<i>Cirsium arvense</i>
10	<i>Trifolium repens</i>		{ <i>Urtica dioica</i>
5	{ <i>Cirsium arvense</i>		{ <i>Rumex sanguineus</i> (?)
	{ <i>Festuca rubra</i>	10	{ <i>Ranunculus repens</i>
			{ <i>Geranium robertianum</i>
			{ <i>Prunella vulgaris</i>
			{ <i>Galium aparine</i>

The greater variety in the flora of the drier land *B* over that of the wetter *A* is fairly well marked.

The reclaimed lands joining the "island" to the mainland have, perhaps, a special interest, as some of them at any rate are in a more advanced state of reclamation than the foregoing. For purposes of comparison the approximate composition of the vegetation on the high ground immediately facing the mainland is given.

High grassland opposite mainland		Dry reclaimed marsh near mainland	
Trifolium repens	} Very abundant	Agrostis alba	} Very abundant
Holcus lanatus		Holcus lanatus	
Dactylis glomerata		Trifolium repens	} Abundant
Alopecurus pratense		Ranunculus repens	
Cynosurus cristatus	} Abundant	Plantago major	} Frequent
Cirsium arvense		Rumex nemorosus	
Plantago media	} Frequent	Ranunculus acris	
Trifolium pratense		Potentilla anserina	
Campanula rotundifolia	} Occasional	Juncus communis	Occasional
Ranunculus acris		Bellis perennis	Rare
Prunella vulgaris	} Rare		
Rumex nemorosus			
Achillea millefolium			
Centaurea nigra			
Wet reclaimed marsh near mainland			
Juncus communis	Very abundant		
Agrostis alba	} Abundant		
Potentilla anserina			
Holcus lanatus	Frequent		
Ranunculus acris	} Occasional		
Lotus corniculatus			
Rumex nemorosus			
Trifolium repens			

III. TRANSITION VEGETATION (UNRECLAIMED).

The inlet marked *D* on the map displays a natural salt-marsh vegetation. A typical piece is represented by the following:

20 %	<i>Statice Limonium</i>	5 %	<i>Samolus Valerandi</i>
20 %	<i>Festuca rubra</i>	5 %	<i>Suaeda maritima</i>
10 %	<i>Salicornia herbacea</i>	30 %	Rocks
10 %	<i>Aster Tripolium</i>		

A line transect from the river (or sea) side of this to the beginning of cultivation yielded the following sequence of plants:

SEA END		
Salicornia herbacea	Festuca rubra	Spergularia sp.
Spergularia sp.	Statice limonium	Spergularia sp.
Statice limonium	Samolus valerandi	Beta maritima
Suaeda maritima	Armeria vulgaris	Agropyrum caninum
Salicornia herbacea	Aster tripolium	Beta maritima
Spergularia sp.	Plantago maritima	Sonchus arvensis
Suaeda maritima	Chenopodium rubrum	BEGINNING OF
Samolus valerandi	Suaeda maritima	CULTIVATION

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What appears to the writer to be a particularly interesting comparison is afforded by the two following transects taken just outside and just inside the sea-wall of the marsh marked *E* on the map.

Outside Sea Wall	Inside Sea Wall
Green Alga [Rhizoclonium?]	Salicornia herbacea
Salicornia herbacea	Plantago maritima
Festuca rubra	Glyceria maritima
Samolus valerandi	Samolus valerandi
Aster tripolium	Spergularia sp.
Festuca rubra	Glaux maritima
Salicornia herbacea	Glaux maritima
Spergularia sp.	Festuca rubra
Statice limonium	Trifolium repens
Festuca rubra	Carex vulpina
Plantago maritima	Luzula campestris
Suaeda maritima	Festuca rubra
Statice limonium	Potentilla anserina
Festuca rubra	Lotus corniculatus
Chenopodium rubrum	Centaurea nigra
Aster tripolium	Festuca rubra
Statice limonium	Trifolium pratense
Festuca rubra	Leontodon hispidus
Beta maritima	Ranunculus acris
Poa annua	Juncus communis
Potentilla anserina	Festuca rubra
Matricaria inodora	Carex vulpina
Rumex nemorosus	Bellis perennis
Festuca rubra	Cynosurus cristatus
Plantago coronopus	Holcus lanatus
	Ranunculus repens
	Cirsium arvense
	Spiranthes autumnalis

As far as could be ascertained Tansley's view (3, p. 68) appears to be borne out that "there is no good evidence that salt marsh can develop by the mere accumulation of silt or humus, without human assistance, into a non-maritime vegetation."

In conclusion I wish to thank Mr E. Standish O'Grady, of Little Island, for his very kind permission to move freely about his property; Mr P. Tate, of the Botany Department, University College, Cork, for his very courteous help in the identifications of some grasses; Mr Michael Twohig for placing his topographical knowledge of the locality so freely at my disposal; and my son Andrew, without whose untiring help the work could not have been accomplished. I have received the kindest help from Prof. H. A. Cummins and Mr J. O. Jagoe, of the Botany Department, University College, Cork, in the re-identification, which was thought desirable, of a few of the species included in the lists.

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- (3) **Tansley, A. G.** *Practical Plant Ecology*, 215, 68. London, 1923.
- (4) **Warming, E.** *Oecology of Plants*, Eng. ed. 231. Oxford, 1909.

NOTICES OF PUBLICATIONS OF GENERAL BEARING

THE PLANT AS AN ECOLOGICAL INSTRUMENT.

- (1) **Clements, F. E. and Weaver, J. E.** "Experimental Vegetation." *Carnegie Instit. Washington Publ.* **355**, 1924.
- (2) **Clements, F. E. and Goldsmith, G. W.** "The Phytometer Method in Ecology." *Ibid.* **356**, 1924.

These two papers, from slightly different aspects, embody the results of an attempt to use plants, or plant communities, as the best measures of reaction to the habitat, in ecological studies. While the value of methods based on this ideal will be obvious, it is equally clear that considerable work is required before suitable methods are evolved, and we may hope that these are to be only the first of a series of papers dealing with this subject. In the first paper, the subject of study is the North American grasslands, the object being to estimate the relative importance of the various vegetation units and their inter-relationships. The methods employed are: (1) sowing seeds, (2) planting seeds or propagules, (3) planting seedlings, (4) transplanting adult plants of various ages, (5) transplanting small communities or portions of communities. In short, these methods aim at observing migration and the subsequent development of vegetation, but under controlled conditions. Accessory to these basic methods are the use or modification of the various factors which may play on the developing plants or vegetation, particularly competition, destruction by animals and the various physical factors. Along with these are checks by instruments and phytometers of the habitat factors. Various methods of altering the physical factors or reducing or modifying competition are employed, of which the simplest and most satisfactory prove to be: (1) sowing on the surface in the midst of natural vegetation; (2) sowing or planting in trenches, by which competition is prevented for a short time; (3) sowing or planting in denuded areas, which eliminates competition for a much longer period, but which makes the water relations less favourable while improving the light relations; (4) transplanting adult plants, either into living cover or into denuded areas; (5) improving the conditions for germination and establishment, by watering, shading, draining or thinning.

The material used included a great variety of grasses, "forbs" (herbs other than grasses), shrubs and trees. These were germinated or transplanted at four climatic stations, representing typical conditions in each of the four main grassland communities between the Missouri River and the Rocky Mountains. A number of edaphic stations represented the various edaphic conditions at each of the climatic stations. It is impossible to summarise adequately the enormous amount of material provided by these experiments, but the results indicate quite clearly that germination and growth of practically all species are reduced as the climatic conditions become drier (i.e. going westwards in the prairie region). The authors therefore regard rainfall and holarid as all important, the other factors in plant growth being secondary. On the other hand the luxuriant vegetation in low prairie—associated with more humid conditions—had a decided effect in reducing the establishment of introduced plants, largely through the reduction in light intensity with which the seedlings

had to contend. The possibility of tree growth under natural conditions on stabilised grasslands appears to be almost nil, since the seedlings are shaded out in the lowlands and destroyed by drought in the uplands.

In the second paper, by Clements and Goldsmith, attention is directed more towards the examination of the effects of the various physical factors by means of *phytometers*, that is, cultures of similar plants of one species in the different habitats considered. The methods employed are described in detail, the plants used being chiefly sunflower and wheat, grown in containers which were sealed to allow of measurements of water loss. The principal comparison made is that between the growth of the phytometer plants at three stations near Pike's Peak, Colorado, designated *plains*, *montane* and *sub-alpine* stations, the natural vegetation of the three main stations being mixed prairie, mixed coniferous forest, and spruce forest respectively. The transpiration per square decimetre of leaf area was highest on the plains and lowest at the sub-alpine station, but the montane station was generally the most favourable for leaf area and stem diameter. Stem length of sunflowers, however, was greatest on the plains. Similarly, there is much variation in the weight of plant produced. Generally, however, sunflowers and beans made best growth on the plains, while wheat and oats did best at the montane station. The water requirement, namely, the amount of water used in the production of 1 gm. of dry material, as defined by Briggs and Shantz, normally decreases with the increase in the altitude at which the plants are grown. A further comparison between the dry warm (*xerocline*) side of a canyon, and its cool moist side (*mesocline*), showed that the former, in its effect on sunflower growth, resembled the plains region—while the mesocline presented typical montane conditions. These results make it clear why the south slope is covered with scrub and grassland dominants of the plains while the north slope is dominated by characteristic montane forest.

Some interesting general conclusions are worthy of notice. Transpiration does not appear to vary consistently with any single instrumental record. No better correlation exists between transpiration and evaporation from a white cylindrical atmometer cup than between transpiration and average temperature. This is to be expected when the composite nature of the factors affecting water loss from a plant is considered, and it is a conclusion which seems to justify the statement that when phytometers are used they are, or may be, a sufficient measure of the factor-complex and render recording instruments unnecessary except in the most elaborate installations. This would seem to be particularly true when the water relations of plants are under consideration—and phytometers such as those employed by Clements and Goldsmith are clearly much more adequate than the rather unsatisfactory atmometers at present in use. The experience of the reviewer suggests that an additional measurement might profitably be made when the phytometer plants have grown for a whole season and their water relations are being estimated. This measurement is the water content of the plant, perhaps most readily expressed by dividing the fresh weight by the dry weight. A brief reference is made in the text to one case in which this ratio varied but the data are not given in the tables.

One fact emerges very clearly from a study of the data—that growth, as measured by increased dry weight, usually shows very little relation to the water loss or water requirement. The authors show that sunflowers and beans normally grow best at the *plains* station, while wheat and oats are most successful at their *montane* station, and they suggest that the former plants have a higher temperature optimum. An analysis of this temperature effect would have proved of great interest, for on the present evidence it seems to be of far greater importance than transpiration alone—which varied in the same way at the different stations whatever the species of plant used. The apparent lack of connection

between transpiration and growth in these observations certainly demonstrates the need for standardised plants for phytometer work. A complete study of a suitable standard species grown under a wide range of environmental conditions is required before the phytometer can rank as an instrument of precision. The value of the method as an aid to the study of vegetation is, however, amply demonstrated by the papers under consideration.

W. H. PEARSALL.

SAP DENSITY AND WATER SUPPLY.

Korstian, C. F. "Density of Cell Sap in relation to Environmental Conditions in the Wasatch Mountains, Utah." *Journ. Agric. Res.* **28**, pp. 845-907. 1924.

This is an investigation undertaken with the object of gaining further insight into the relations of plants to the conditions of the environment, especially in regard to forestry and forest regeneration. In this problem the water relations take a very prominent place, and an investigation of the osmotic forces of the cell sap was considered as affording useful information. The work was carried on in the Wasatch Mountains in Utah, and the area covered extends from Sage Brush on the one hand, to the montane tree limit on the other, at altitudes varying from 5000 to 11,500 feet, and covering a great variety of physiographic features. The material tested was collected in sealed tubes and the sap extracted by the freezing method. A special convex cup and concave presser were used. Care was taken to avoid water loss after collection. Data are given of the environmental conditions of the chief habitats studied, especial attention being paid to temperature, soil moisture, and evaporation.

A considerable number of plants were investigated; in most cases samples of each species being collected from more than one locality. The table of the results of determinations of the osmotic power of the cell sap occupies 23 pages. In the discussion of the results emphasis is laid on the correlation between sap density and water supply. The density is lower in the roots where these have been tested. The value obtained for any plant is not a constant. There is a daily fluctuation, a rise in the forenoon and a fall towards evening. Sun plants gave higher values than those in shade. A close relation seems to exist between photosynthesis and sap density. Large plants, trees, etc., always gave higher values than herbaceous species. In a tree there is an apparent osmotic gradient, the lower leaves having lower values than those higher up.

A seasonal fluctuation of density was also demonstrated. Young leaves have a uniformly lower value than old ones. Otherwise the seasonal variation follows the habitat conditions: the maximum density occurs in the dry part of the summer. In winter a variable state of things was found. Conifers had low values while evergreen shrubs had high ones. This difference is apparently directly correlated with the nature of the food reserves; in conifers in winter fats and oils appear in quantity in the leaves, while in evergreens starch was converted to sugar.

Individual species showed great variation in value according to the habitat. Average results of all the plants tested in each habitat gave results which accord very closely with the degree of xerophily of the habitat. Averages of the plants from successional stages showed a progressive decrease in density as the succession advances. The density showed

some relation to structural features; those plants with structural features tending to a reduction of transpiration, or with water-storage tissue, had uniformly low figures. The parasites studied had higher values than their host plants.

Capacity to resist injury from drought, frost or other factors bore a close relation to the osmotic power of the cell sap. The higher the value the hardier was the plant.

R. S. A.

MEASUREMENT OF WATER LOSS.

Weaver, J. E. and Crist, J. W. "Direct Measurement of Water Loss from Vegetation without disturbing the Normal Structure of the Soil." *Ecology*, 5, 2, pp. 153-170. 1924. Pl. III.

The objection to the ordinary method of determining water loss is that the plant is growing in a disturbed soil that is very different from that of the field. Further, unless any large containers are used the root systems are seriously cramped. A method has been devised for measuring the water loss without disturbing the soil. Metal cylinders of one square foot cross sectional areas are used to cut out an area of vegetation and then iron cylinders of three foot length are forced tightly over the column of soil. This is then excavated, the lower end sealed up, and the whole sunk in a suitable trench. The containers are weighed before being put in the trench and at the end of the experiment. In this way samples of undisturbed natural vegetation or of crops can be studied.

Experiments were carried out with these methods on the short grass plains, on mixed prairie, and on prairie vegetation. During the experiments the containers with their columns of soil were protected from rainfall. Water was added carefully and slowly so as to give an even distribution through the soil. Direct loss of water from the soil and from soil covered by dead plants was determined. Crop plants were found to give off more water than the native vegetation. The latter gave off sufficient in the period of the experiment to furnish the mean precipitation. The advantages of the method for the study of the problems of the relations of the plant to soil and soil moisture are very great as these can be tackled with natural conditions for the absorbing organs.

R. S. A.

ANIMAL ECOLOGY.

Alkins, W. E. "The distribution of *Pisidia* in the Oakamoor district of the Churnet Valley." *Trans. North Staffs. Field Club*, 1924-25.

With the help of A. W. Stilfox the author has made a detailed study of the ecological relations of the eight species of these small bivalve mollusca which occur in a restricted area in North Staffordshire. The habitats include parts of a disused canal, streams, ditches, ponds and a marsh, and the transition is traced from the river-canal association of *P. sub-truncatum*, *nitidum*, *henslowianum* and *milium* to the ditch-marsh society of *P. casertanum* and *personatum*.

A. E. B.

NOTICES OF PUBLICATIONS ON BRITISH VEGETATION

A BRITISH WOODLAND NEAR LONDON.

Marriott, St John. *British Woodlands as illustrated by Lessness Abbey Woods.* London: Routledge and Woolwich Pioneer Press, 1925. Pp. xviii + 72, with photographic plates of scenery and a sketch map.

This is a very interesting and praiseworthy little booklet, inspired by the "Regional Survey" movement through the agency largely of Mr C. H. Grinling, and promoted by various local scientific societies. There is a historical, topographical and geological introduction by Mr Grinling, and the body of the work consists of Part I, including a vegetational survey (illustrated by the sketch map), a complete list of plants comprising *all* the terrestrial groups of the plant kingdom, and Part II, including lists of mammals, birds, reptiles, amphibia, fishes, galls, lepidoptera, molluscs and fossils.

Mr Marriott is a keen field naturalist and he has invoked the aid of many specialists, so that the determinations of species may be taken as really trustworthy. His vegetation survey (illustrated by charts of special localities) brings out very clearly the effect of the various soils on the flora and vegetation. To the ordinary seasonal "aspects" of vegetation, Mr Marriott happily adds a "hiemal" aspect. The wood is evidently semi-natural, though there has been a fair amount of planting and some other disturbances of the natural relationships of the vegetation.

It is much to be desired that other local societies should follow this excellent example, especially where areas of natural and seminatural vegetation still exist in the neighbourhood of large towns and cities, before it is too late. Such accounts provide indispensable data for the student of vegetation and of ecology and natural history in general, as well as stimulating local pride in natural areas of country near great centres of population, areas which are not yet spoiled or destroyed and which in some cases may still be saved.

A. G. T.

A SCOTTISH AREA.

Patton, Donald. "The Vegetation of the Tinto Hills." *Ann. of the Andersonian Naturalists Society*, 4, 2. Glasgow, 1925. Pp. 30-51.

The Tinto Hills in Upper Clydesdale, Lanarkshire, belong to the Southern Uplands of Scotland. Tinto itself reaches a height of 2335 feet, the other summits ranging from 1472 to 1925 feet. The annual rainfall exceeds 45 inches in places, and mist is very prevalent. The mean January temperature is about 35° F.; July, 57° F. The whole region, including the summits, was glaciated and there is a thick layer of Boulder Clay round the bases of the hills. The Clyde has cut this away and formed a rich alluvial tract. The hills themselves are felsite.

The author divides the region into a lowland division, including (1) Aquatic, (2) Gravel, (3) Alluvium, (4) Boulder Clay, and a hill division, including *Calluna-Pteridium*, *Calluna-Erica cinerea* and *Calluna-Vaccinium* zones. The lowland zone has been much altered by farming. The Boulder Clay has been extensively limed, and there are many introduced plants. The heavier clay at higher altitudes has also been limed and bears good pasture of native grasses and sedges. The whole of the hill division may be regarded as a *Calluna* heath, this species extending to the summits, though much less abundant than at lower levels. In the *Calluna-Vaccinium* zone *V. myrtillus* gives place upwards to *V. vitis idaea*, and there is an abundance of lichens and mosses.

The paper concludes with a tabular list of the flora arranged under the zones given, to which is added some account of "Railway vegetation."

A. G. T.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

FINNISH FORESTS.

- (1) **Cajander, A. K.** "Ueber Waldtypen." 1909. *Acta forestalia fennica*, 1.
- (2) **Cajander, A. K.** "(a) Über die Verteilung des fruchtbaren Bodens im Finnland und über den Einfluss dieser Verteilung auf die wirtschaftlichen Verhältnisse im Lande. (b) Was wird mit den Waldtypen bezweckt?" 1923. *Ibid.* 25.
- (3) **Cajander, A. K.** and **Iivessalo, Y.** "Ueber Waldtypen II." 1921. *Ibid.* 20.
- (4) **Iivessalo, Y.** "Vegetationsstatistische Untersuchungen über die Waldtypen." 1922. *Ibid.* 20.
- (5) **Iivessalo, Y.** "Ein Beitrag zur Frage der Korrelation zwischen den Eigenschaften des Bodens und dem Zuwachs des Waldbestandes." 1923. *Ibid.* 25.
- (6) **Iivessalo, Y.** "The Forests of Finland." 1924. *Communicationes ex Instit. Quaest. Forest. Finland.* Editae 9.

The results of the Finnish Forest Survey appear to have reached a stage at which a general outline of Finnish woodland ecology can be obtained. The survey deals with the results of estimations of the forest vegetation, tree production and soil character, along thirty-nine survey lines, twenty-six kilometres apart and running south-west to north-east over the whole of Finland. On the data obtained from these survey lines, a very complete description of the forest resources of the country is possible. The degree to which the country is still covered by its native vegetation may be gauged from the fact that 73 per cent. of the area is still forest, and about 15 per cent. is waste land, chiefly *Sphagnum* bog (7 per cent.) and "pine swamp" (4 per cent.). The composition of the forest naturally varies very considerably with the variations in soil and climate. Pine (55) and spruce (25) dominate 80 per cent. of the forest land, the remainder being chiefly birch forest (17 per cent.), although alder and aspen may also be dominant in the south. Birch is more prevalent in the north owing to its ability to grow in the barren *fjeld* regions.

The distribution of the trees is otherwise largely determined by the nature of the soil, and a number of ground flora types are recognised, each of which usually occurs on a characteristic type of soil. Excluding local modifications, the chief forest types are:

1. *Sanicula* type (ST). With numerous herbaceous species like *Paris quadrifolia*, *Milium effusum* and *Majanthemum bifolium*. Occurs on calcareous soils in the south-west.
2. *Oxalis-Majanthemum* type (OMAT). Smaller thin-leaved species more abundant. On fertile soils in the south.
3. Fern type (FT). In valleys on soils like 2.
4. *Oxalis-Myrtillus* type (OMT). On clayey or damp soils.
5. *Myrtillus* type (MT). With an almost continuous covering of mosses, chiefly *Hylocomium* spp. Found on only moderately fertile soils of morainic origin.
6. *Vaccinium* type (VT). *V. vitis-idaea* and *Hypnum parietinum* most abundant. Very widespread on morainic matter.
7. *Empetrum-Myrtillus* type (EMT). Common in the north.

8. *Calluna* type (CT). On the drier and coarser morainic soils.

9. *Cladina* type (CIT). Dry sandy soils in the north.

While there is no hard and fast relation between these types and the tree dominants, nevertheless pine is the normal dominant along with the heathy types of ground flora 6-8. Spruce is the typical dominant when the forest type is 4 or 5, although pine covers considerable areas, about one quarter, of these soils also. The soils occupied by forest types 1-3 are covered by the small areas of deciduous forest, and in these pine is normally absent. Much of the deciduous forest seems, however, to be of secondary origin. Forest destroyed by fire and deserted clearings are normally colonised by birch, aspen or *Alnus incana*. Alder woods are almost restricted to the damper lands which have been burned over for agricultural purposes.

The *Vaccinium* type, with pine dominant and spruce frequent, is probably the most widely spread type of forest, although the *Myrtillus* type is more important from the point of view of timber yield, as it is nearly as widespread and is much more productive. The relative areas, timber yields and soil types are most conveniently summarised in the following table, amplified from Cajander (2). The figures for lime and total nitrogen are relative, the detailed figures being given by Ilvessalo (4), who shows that the lime and total nitrogen—of the various soil factors—possess the highest degree of correlation with the timber production.

Forest type	Distribution as per cent. of forest area		Soil type (upper 20 cm.)		Annual increase of normal		No. of species of Phanerogams
	North	South	Lime (CaO)	Total N	Pine stands	Birch stands	
2. OMaT }			{ 140	223	—	185	158
4. OMT }	1	6	{ 117	137	115	117	119
5. MT	4	38	100	100	100	100	100
6. VT	18	31	79	71	83	83	73
7. EMT	26	—	—	—	(32)	—	—
8. CT	10	7	54	64	52	—	41
9. CIT	9	—	36	34	27	—	20

The correlation between the lime content of the soil, the timber yield and the relative number of flowering plants as revealed in this summary is very striking, and it suggests a high degree of dependence of the plant covering upon the lime content of the soil.

W. H. P.

CORAL REEFS OF CUBA.

Uphof, J. C. Th. "The Plant Formations on the Coral Reefs along the Northern Coast of Cuba." *Amer. Journ. Bot.* 11, pp. 409-416, 1924.

The reefs form masses of stone near the shore or at some distance out. In height they vary from 30 metres down to about 2 metres or less above the sea. From sea-level to a height of 3-5 metres constant washing by sea water occurs. The plants are not only halophytic but able to endure a very calcareous substratum. The Algal flora is briefly mentioned, but this has not been fully worked out. Of low plants, those that grow nearest the sea water are typical halophytes with more or less succulent leaves or stems, *Sesuvium microphyllum*, *Phylloxerus*, and *Salicornia*, with *Distichlis spicata*. Other species predominate on higher reefs, e.g. *Conocarpus erecta*, which is very stunted near the shore, but almost a tree when protected. At a distance of 20-30 metres, where sand has collected on the reef, a much more luxuriant and varied vegetation occurs, consisting of plants without marked halophytic features.

R. S. A.

VEGETATION OF THE ARID PORTIONS OF NORTH AMERICA.

Shantz, H. L. and Piemeisel, R. L. "Indicator Significance of the Natural Vegetation of the South-Western Desert Region." *Journ. Agric. Res.* **28**, p. 721, 1924.

The region considered is in southern California and Arizona with part of Nevada and Utah. The whole area is arid, having a rainfall of from 2-7 inches in the valleys, though rising to 15 inches on the upper lands. Two areas are considered in some detail, one in California, the other in Arizona, and the plant communities correlated with the physical factors. Then the communities are considered in their wider aspect and the general range of factors controlling each is given. The chief communities are:

1. *Yucca* and *Cactus* Association, which occurs on hill slopes. This is replaced by Giant *Cactus* and Paloverde (*Cercidium torreyanum*) in Arizona.
2. Creosote Bush (*Covillea glutinosa*) Association, which is the most widespread. This occurs on light soils of about 4 ft. depth, which are permeable and well drained and which become very dry in summer. The soil is not saline.
3. Desert Sage (*Atriplex polycarpa*) Association. This occurs at lower levels with higher temperature. The soil is finer and has a greater moisture-holding capacity than that of the creosote bush association. The soil is generally liable to floods in winter, but is very dry in summer. The available water is less than in the former association; the salt content is higher but small.
4. Mesquite (*Prosopis glandulosa*) Thicket. This occupies the bottoms of valleys. The soil is like that of the desert sage association but has a higher water table so that available water is always present in the first 4 ft. of soil. Salinity is higher.
5. Narrow-leaf Saltbush (*Atriplex linearis*) Association. This occupies low flat depressions with a heavy compact soil which becomes very dry in summer. The salt content is higher, especially in the deeper layers. This community indicates a much shallower soil than desert sage.
6. Salt Grass (*Distichlis spicata*) Association. This is of limited extent. It occurs in very saline soil with a high water table.
7. Washington Palms (*Washingtonia filifera*) occur as scattered groups or communities round springs or streams.
8. Pickleweed (*Allenrolfia occidentalis*) Association occurs at the bottoms of valleys where an excess of salt is present in the surface layers of soil.
9. Mesquite (*Prosopis glandulosa*) and Chamiso (*Atriplex canescens*) is an association characteristic of sandhills.
10. Arrowweed (*Pluchea sericea*) and Saltbush (*Atriplex lentiformis*) Association is a community of local occurrence. It is present in soil like that of the pickleweed association, but with a coarse subsoil and a lower salt content below the surface.
11. Sceptweed (*Dondia* spp.) Association occurs in level valley bottom with a high water table and a high salt content.
12. Bare flats occur scattered through the lower parts of the valley. The soil is heavy and the water stands on the surface after rains, but in dry weather cracks freely. The salt content is very high. These flats are either devoid of plants or have a very scattered vegetation in the most favourable places near the edges.

Each of these associations is described, the botanical features given, and a full statement of the chief physical factors. The description of the communities is followed by a discussion of the relations to climatic factors and especially to rainfall and temperature. A correlation is also made between the natural vegetation and the character and productiveness of the

land. In this connection it is pointed out that the various associations have a wide range of conditions, so that it is necessary to know more than the vegetation type before any interpretation of the potentialities of the soil can be made. Some details of the association must be given; in fact if a primary ecological survey is made, a fairly accurate measure of land values is reached.

Throughout the paper there are full tables of soil analyses, water contents and physical and climatic factors. The paper is illustrated by ten plates, each containing two photographs of high quality.

R. S. A.

Aldous, A. E. and Shantz, H. L. "Types of Vegetation in the Semiarid Portion of the United States, and their Economic Significance." *Journ. Agric. Res.* **28**, pp. 99-128, 1924.

The principal vegetation types occurring west of the hundredth meridian are enumerated, and their distribution and conditions briefly indicated. Notes are also given of the possibilities for crop production, either of grain or forage plants, and for grazing. Altogether 102 vegetation types are enumerated. These types are then grouped according to their possibilities for dry farming, for grain production, and for forage plants. A tabular key of the carrying capacity for stock is given; and the geographical distribution according to regions which cover practically the whole range. There are 32 photographs on 16 plates in illustration. The paper, though merely an outline scheme, is valuable in showing the uses of ecology for practical purposes and suggests lines that might well be adopted in other countries, where the agricultural community is advancing to untouched regions. A preliminary ecological survey and land classification of this kind would certainly result in fewer failures and ultimately in much greater economy of production.

R. S. A.

VEGETATION OF ARID AUSTRALIA.

- (1) **Osborn, T. G. B. and Wood, J. G.** "On the Zonation of the Vegetation in the Port Wakefield District, with special Reference to the Salinity of the Soil." *Trans. Roy. Soc. South Aust.* **47**, 244, 1923.
- (2) **Osborn, T. G. B. and Wood, J. G.** "On some Halophytic and Non-halophytic Communities in Arid South Australia." *Ibid.* 388, 1923.
- (3) **Wood, J. G.** "On Transpiration in the Field of some Plants from the Arid Portions of South Australia, with Notes on their Physiological Anatomy." *Ibid.* 259, 1923.

These three papers form part of what promises to be a detailed investigation of the vegetation of the arid portions of South Australia. A very large proportion of this region is occupied by an open community of small shrubby plants belonging to the family Chenopodiaceae. There are many species of *Atriplex* (Saltbush) and *Kochia* (Bluebush)¹. These communities, though of such wide extent, have either been neglected by plant geographers or treated as communities of Halophytes. This view is based on the systematic position of the plants, the Chenopodiaceae containing a large number of halophytes, and on the low lying nature of the country they inhabit and the fact that in most cases the bottom water is decidedly salt. The present papers mark the commencement of a detailed study of these communities.

1. In the first a study is made of the zonation of communities passing from those under the influence of sea water at the coast up to Saltbush communities further inland. Excluding the Mangroves, which are treated as belonging to a separate formation, a view that need not be considered at the moment, four communities are recognised and briefly

¹ "Saltbush" is a general name applied to various low shrubby species of *Atriplex*, *Rhagodia* and *Kochia*, "Bluebush" to white tomentose species of *Kochia*, e.g. *K. sedifolia*.

described. The characteristic plants of these are *Arthrocnemum arbuscula*, *A. halocnemoides*, *Atriplex paludosum* and *A. stipitatum*. These communities show a decreasing water content of the soil and a decreasing salt content, both of total salts and of sodium chloride. The figures of the saltbush communities are so small for salts, 0.3–2.8 per cent., that they cannot be regarded as truly halophytic.

2. This paper deals with some of the communities of these Chenopodiaceous plants in the inland portions; communities of Saltbush (*Atriplex vesicarium*), Mallee (*Eucalyptus oleosa*) with Saltbush, *Kochia planifolia* and Bluebush, *Kochia sedifolia*, are described and analyses of the soils of each given. The soils are all exceedingly dry, 2–8 per cent., with a low salt content, 0.1 to 0.18 per cent. total salts of which 0.3 to 0.6 per cent. is NaCl. The reaction is slightly on the alkaline side of neutral (pH 7.4 to 7.7). By contrast with these, communities in two salt lakes are described; the first is a gypsum lake where *Arthrocnemum halocnemoides* var. *pergranulatum* is the chief plant. The soil here has 4.97 per cent. of soluble salts of which 0.68 per cent. is NaCl. The reaction is more alkaline, pH 8.2. This community gradually merges into the saltbush and intermediate soil conditions are found. In another lake where the soil contained 6.6 per cent. of soluble salts with 3.52 of NaCl, *Pachycornia tenuis* formed a pure community. These last two, which are decidedly halophytic, are sharply marked off from the others both in habitat and soil and also in general facies. The shrubby species of *Atriplex* and *Kochia* are considered as forming the typical flora of arid regions in South Australia and are compared to the Karroo flora of South Africa.

3. This paper deals with the physiological anatomy of some of the plants in these communities and also with the transpiration under field conditions. Transpiration was measured by means of burette potometers according to Lloyd's method. Of the plants examined, three types of transpiration curve are noted: (a) *Casuarina lepidophloia*, which has a relatively high rate and a curve which follows closely that of evaporation. (b) *Geijera parviflora* and *Pholidia scoparia*, which have a low transpiration rate. While the maxima correspond to the maxima for evaporation there is not close agreement for minor fluctuations. (c) The third group contains the shrubby Chenopodiaceae *Kochia sedifolia*, *Atriplex vesicarium* and *Rhagodia gaudichaudiana*. The transpiration curves in these are all very similar. The rate is practically constant at a low figure during the day with a fall at night which takes place later with *Kochia* than the others. These Chenopodiaceous plants have a dense covering of hairs, vesicular in *Atriplex* and *Rhagodia*; *Kochia* has a thick felt of hairs which probably functions for water absorption.

R. S. A.

Wood, J. G. "The Relations between Distribution, Structure and Transpiration of Arid South Australian Plants." *Trans. Roy. Soc. South Australia*, 48, pp. 226–235, 1924.

This paper is a continuation of the author's work on the water relations of plants in South Australia. The present account deals with experiments carried out on the central plain of Australia at Curnamona, which is some miles south of Lake Frome. The rainfall here is about seven inches, but very uncertain. Six species are studied, three being plants which are "character" species of the plains, two are plants from watercourses and the last is a parasite (*Loranthus quandang*). An account is given of the anatomy of the leaves. These plants show very different transpiration rates; the plains species have a much lower rate, especially so in the case of the Saltbush, *Kochia planifolia*, which gives an almost flat curve for a 24-hour period. *Kochia* is here the most prominent plant and appears the best suited to the conditions. In addition to its other features the leaves have a thick covering of hairs. The stream bed plants show a higher rate, one, a shrubby Acacia (*A. victoriae*), only slightly so, but the other, *Senecio magnificus*, a herbaceous plant, shows a very uneconomical usage of water. Especially interesting is the parasite *Loranthus*, which has a much more rapid transpiration rate than its host plant.

R. S. A.

NEW SOUTH WALES.

Brough, P., McLuckie, J. and Petrie, A. H. K. "An Ecological Study of the Flora of Mount Wilson. Part I. The Vegetation of the Basalt." *Proc. Linn. Soc. of New South Wales*, 49, pp. 475-498, with Plates LVII-LX and 5 figures in the text. 1924.

With a view to stimulating ecological work in Australia, the Sydney University Botanical Society in 1923 initiated a study of the vegetation of Mount Wilson. The present paper, which embodies some of the results obtained, is largely of the nature of primary survey, which has been carried out for the purpose of studying the relationships and distribution of the various plant communities, and also to lay a foundation for future intensive studies.

After a brief notice on the general features of the Australian flora the authors proceed to discuss the origin of the flora of New South Wales and in particular of Mount Wilson. It is composed chiefly of three elements, an endemic flora consisting largely of *Eucalyptus* forests and occupying the greater part of the state; a Malayan flora finding its chief expression in Rain Forest; an Antarctic flora which occurs as scattered individuals in certain regions. A study of the fossil evidence tends to show that the Malayan flora emanated from the north in the early Tertiary and spread through the greater part of the continent, later being invaded by the endemic flora which originated elsewhere on the continent. Subsequent changes in the physiography of the country resulted in the Malayan flora receding to sheltered habitats controlled by markedly favourable edaphic factors, whilst the endemic flora became adapted to a xerophytic habitat. On Mount Wilson, which is one of a series of residual Tertiary basalt outflows and consists of a sandstone ridge with frequent caps of igneous rock, the Malayan flora occupies the sheltered slopes of the basalt caps and the sandstone gullies, the endemic flora being found on the sandstone plateau. The present paper deals with the vegetation occupying the basalt caps.

Four chief types of vegetation are distinguished: the *Ceratopetalum-Doryphora* Forest; the *Eucalyptus-Doryphora* Forest; the *Eucalyptus-Alsophila* Forest; the *Eucalyptus-Pteridium* Forest. These four, however, are actually variations of two main groups, the *Eucalyptus* Forest on the sandstone and the *Ceratopetalum-Doryphora* Forest on the basalt.

Each of these four types, or "associations" as they are termed, is then discussed in detail. Their habitat, and structure and physiognomy are described and their floristic composition enumerated under their respective strata. In the *Ceratopetalum-Doryphora* association an interesting note is recorded on *Quintinia sieberi*. Young plants of this epiphyte become established among the leaf bases and tangled adventitious roots on the trunks of tree-ferns. Subsequently the roots of the *Quintinia* reach the ground where they become established. This is the only case of hemi-epiphytism encountered in the Rain-Forests at Mount Wilson.

The discussion of the effect of fire on the different types of forest provides some interesting information. Round every junction of these types the vegetation bears "all the indications of having been recently burnt. The fire has crept up to the edge of the basalt, has in places passed through the *Eucalyptus-Alsophila* association, but has never transgressed the humid Rain-Forest." The bush fire is stated seldom to destroy the climax associations, but profound alterations usually occur in the lower layers, often resulting in a pure community of *Pteridium aquilinum*.

Interesting methods of showing the distribution are employed in the text-figures. In the examples of chart and belt transects the idea is to convey a "bird's-eye view" impression. The various components of the vegetation are indicated by symbols but the canopy of the larger components is also outlined, the lower layers showing through or displaying

graphically their denser grouping where not overshadowed by a canopy. In the diagram the approximate ranges and frequency of the basalt flora are depicted in rectangular form, the various types of vegetation being set out along a base line. The range of the dominant through the various types is indicated by a band which is broadest when the dominant occurs most frequently and tapers away in each direction as the dominant loses its position.

T. F. C.

Petrie, A. H. K. "An Ecological Study of the Flora of Mount Wilson. Part II. The *Eucalyptus* Forests." *Proc. Linn. Soc. of New South Wales*, **50**, pp. 145-166, Plates XX-XXII, and four figures in the text. 1925.

This second part contains an account of some of the salient features of the *Eucalyptus* forests which constitute the vegetation of the sandstone plateau, and supplements the observations recorded in Part I on the *Eucalyptus* communities of the basalt. The main communities in the area under observation are outlined, observations on their distribution and inter-relationships are recorded and some of the more important problems indicated concerning their adaptations, development and other studies awaiting investigation.

In discussing the general physiognomy of the *Eucalyptus* forest it is pointed out that in most cases the association dominants are species of *Eucalyptus* of which there are some three hundred species in Australia. Despite this the physiognomy is characteristically uniform as the species of *Eucalyptus* all present a xerophytic appearance and possess the same growth form. The open nature of their foliage and the comparative isolation of the trees permits a considerable development of the lower layers of the associations.

An interesting comparison is drawn between the *Eucalyptus* forest and the Rain forest previously described; the former is typically xerophilous; the latter, composed of luxuriant vegetation, is typically mesophilous. The interdependence characteristic of the Rain forest is distinctly lacking in the *Eucalyptus* forest, where epiphytes are scarce and ombrophytes absent. The Rain forest at Mount Wilson, on account of the severity of the climate, is, comparatively, of a poor floristic composition.

It is interesting to find that for the classification of the communities the author has adopted Clements' system with Tansley's conception of climax communities, though it is natural that there are instances where he finds it necessary to consider modifications to suit local requirements. For instance, he states that the structure of the *Eucalyptus* forest is likely to be responsible for many problems connected with the definition of status. It is no uncommon occurrence for one society of shrubs to occur in two different associations, and the typical substratum of a *Eucalyptus* association may occur where the development of trees is inhibited. The result of this is that the shrub-community changes from the rank of a stratum society to that of a definite association.

Two associations, whose dominants always occur in consociations, are distinguished as making up the forest under discussion, together with the *Eucalyptus-Doryphora* ecotone. Their distribution, structure, physiognomy and stratum societies are described. In the comments on the relation of forest fires to these communities it is pointed out that the essential oils of an inflammable nature contained in the leaves do not of themselves make burning possible as the fires travel mainly through the substratum where the percentage of oil-containing types is not high. It is rather the low moisture-content of the leaves that favours the fires.

An interesting discussion is also given on the relation of the dehiscence of fruits to the periodic fires and the effect on the population in the early stages of the resulting subseres.

The latter part of the paper discusses in detail the shrub (stratum) societies of an exposed westerly headland and of the Junction Flora.

The system on which the author is working, as well as the scheme of work determined, is of much interest. It should prove of assistance in indicating to workers on similar problems extending over large areas the means of approach and the development of the first general stages in studies of vegetation.

T. F. C.

CYPERUS ROTUNDUS L. IN INDIA.

Ranade, S. B. and Burns, W. "The Eradication of *Cyperus rotundus* L. (a study in pure and applied botany)." *Memoirs of the Department of Agriculture in India*. Botanical Series, **13**, 93 pp. and 8 plates.

The memoir contains a full description of this troublesome weed and of several series of experiments conducted with a view to establishing some standard method for its eradication. The plant has several interesting features. Its rate of seed production is fairly high but germination is erratic. It survives chiefly by the production of underground tuber-forming rhizomes, some of which are positively geotropic and may reach a depth of 2.5 feet.

Extensive experiments were undertaken to determine the viability of the tubers under varying external conditions. The authors consider that the features in the life cycle which lend themselves to attack are the inability of the plant to flourish in a close community, e.g. in a thick growth of Saun hemp, and the fact that the tubers usually fail to survive after a fortnight at 40° C.—the temperature of the upper soil during the hot season.

The description of the work is very full and the experimental data are given in great—perhaps too great—detail. The outlook of the writers on the plant's life is extremely anthropomorphic, thus a deep-seated tuber is described as "concentrating all its powers in making one supreme attempt to get to the surface and not wasting material on several ascending organs."

Economically the work achieves its object, scientifically it opens up a host of semi-physiological problems which bid fair to be of great interest—e.g. the reaction of the external conditions on the plant's physiological processes, causing some rhizomes to be positively geotropic; or again the reason why one bud develops from a deep-seated tuber and several from one which is more superficially situated. It is to be hoped that the authors may find opportunity for the further autecological investigation of the species.

S. M. W.

ARID SOUTH AFRICA.

Cannon, W. A. "General and Physiological Features of the more arid portions of Southern Africa, with Notes on the Climatic Environment." *Carnegie Institution, Washington*. Publ. No. 354, 1924, pp. 1-159. 31 plates and 13 figs. in the text.

This volume is a companion to the author's work on arid South Australia which was reviewed in this *Journal* two years ago (**12**, p. 338, 1924). The arrangement and treatment of the subject matter are very much the same in the two volumes and several of the general remarks that were made in the former review might be applied equally to the present work.

The area in South Africa which has a more or less markedly arid climate and vegetation is large and the present account makes no attempt to give a complete picture of the region. It is a record of the author's observations made at a series of selected places during his visit to South Africa. This method of treatment of a large area by the description of selected samples has certain inherent drawbacks which are apparent in reading this volume. There is a considerable degree of discontinuity and the relationships of communities to the environment and to one another are lost sight of. In any case, however, Dr Cannon centres attention on representative plants and the adjustment of these to environmental conditions rather than on, indeed almost to the exclusion of, plant communities.

In the first part of the book a general account of the climatic and other features of South Africa are given; such features as temperature, rainfall, wind, and humidity of the air are considered. Under rainfall, special attention is paid to the seasonal distribution and to the occurrence and duration of drought periods. An attempt is made also to determine the amount of the total precipitation which is "effective" and "non-effective." Evaporation was also studied; and for this purpose Dr Cannon introduced a number of porous cup

atmometers of the Livingston type. This was the first time such instruments had been used in the country. These atmometers were established at a number of representative stations, but in most cases they were not running for a sufficient length of time to allow of any generalisations to be made from the figures published. Also the results, such as they are, are to some extent vitiated by the great variability of the instruments when they were restandardised after use. The account of the climatic factors is followed by a very general description of the main types of vegetation and of the botanical regions but in this portion nothing new is added to the accounts previously published.

The description of the author's own observations follows this general introduction, observations which were made at selected stations, in the Namib in South West Africa, and at three stations in the Central and Western Karroo, Beaufort West, Prince Albert Road, and Majesfontein. General descriptions of the vegetation and topography at each station are given, but unfortunately these are so short that it is exceedingly difficult, if not impossible, for a reader, who is unacquainted with the ground, to make any clear picture.

At the Karroo stations quadrat enumerations of the perennial plants were made which give a good indication of the degree of local variation in the flora of these regions. Thus at Majesfontein four quadrats, each 10 meters square, had respectively: 49 individuals, all sclerophylls; 345 individuals, all sclerophylls; 330 (170 succulents); and 397 (213 succulents).

Some notes are given on the root habits: the succulents as a rule have a meagre root system which is mainly superficial although exceptions were noted in *Euphorbia multiceps* and *Pelargonium crithmifolium*, where the main root descended to deep levels and did not form superficial roots. This phenomenon occurs in many other species of *Euphorbia*. The sclerophylls have generally a much larger development of roots. Some cases of root budding are noted.

The next section deals with the structure of the foliar organs of a considerable number of the plants. The leaf structure showed very great variety, and the influence of the environment seems to have been in the direction of the development of xerophytic features on various plans of structure. A summary of some of the features of the families is given, their distribution considered and suggestions as to the lines along which the structural modifications have occurred are put forward.

The final portion deals with the foliar transpiring power of the plants in winter and spring. The observations were made for the most part in the Karroo and the experiments were made by the Stahl-Livingston cobalt chloride method, a method that has great advantages for such field studies. A variety of plants was investigated, succulents, sclerophylls, and some geophytes. While the results are rather fragmentary and were all made in winter, they do show certain features of interest. The index was found to fall during the day; in the sclerophylls the maximum occurred in the early morning; in the succulents it is at night. The maximum itself is in many cases exceedingly low. It is interesting to note, in passing, that a few tests, made on *Welwitschia*, gave a surprisingly high index, which suggests that, in spite of the habitat, this peculiar plant may not be quite so extreme a xerophyte as it is sometimes thought to be.

The volume as a whole leaves the reader with a feeling of lack of satisfaction, almost of disappointment. This is due mainly to the great discontinuity in the treatment of the subject matter. The book is really a series of field notes and not one whole; many subjects are touched upon but of none of them is there anything like a full account, and the passage from one to the other is abrupt. The resulting impression on the reader is of a series of isolated fragments. But, in spite of these drawbacks, which are to some extent inseparable from the methods of study and treatment, Dr Cannon's book should be of value in drawing the attention of botanists, and especially of South African botanists, to an extremely interesting vegetation which presents a very great number of problems for investigation. His results, all of which are necessarily of a preliminary kind, should act as a stimulus to others to undertake detailed work in these regions. The book is illustrated by a number of excellent photographs.

R. S. A.

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VOLUME XV
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WITH TEN PLATES, AND NUMEROUS FIGURES
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THE PHYSIOLOGY AND ECOLOGY OF THE CALCIFUGE HABIT IN *ERIOPHORUM ANGUSTIFOLIUM*

By W. H. PEARSALL AND E. MARJORY WRAY

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INTRODUCTION

THE occurrence of moorland plants on "sour" or lime deficient soils and their absence from more normal or calcareous soils, which are favourable to the majority of plants, has presented a problem which has been of perennial interest to field botanists. While around this problem a variety of speculations has developed, it is perhaps safe to say that none of the explanations advanced to account for the distribution of moorland plants has proved to be entirely satisfactory. It, therefore, seemed that a further study of the subject might prove to be of value, and a starting point for this study was provided by some field observations which suggested that not only calcium deficiency but also a high proportion of potassium and sodium (a high *basic ratio*) might be important factors in the distribution of plants of "sour" soils (16, 17).

Detailed reference to these observations will be made at a later stage. Along with the factors mentioned, "sour" soils (16, 17) usually show a relatively high hydrogen ion concentration as a feature distinguishing them from more normal soils. Since moorland plants may grow on soils or other media which are not markedly acid (Rayner (23), Atkins (2), Pearsall (16, 17)), it seems possible that the hydrogen ion concentration of the rooting medium may not be of predominant importance in determining the distribution of moorland types of vegetation. In any case, these considerations suggested that our preliminary problem was the investigation of the *calcifuge* habit in

2 *The Calcifuge Habit in Eriophorum angustifolium*

terms of (1) the calcium content of the soil solution, (2) its basic ratio, and (3) its acidity or hydrogen-ion concentration.

METHODS

It is obvious that these factors could best be controlled by using culture solutions as the rooting media, and solutions were therefore used throughout in spite of their lack of resemblance to soil conditions. The latter disadvantage was, however, greatly, if not entirely, reduced by the use of *Eriophorum angustifolium* and *E. vaginatum* as the chief culture plants, since these plants normally grow either in water or in extremely wet habitats. Most moorland plants also possess three further disadvantages for this type of culture work. In the first place, they may be difficult to grow from cuttings or seed, or may only grow from cuttings at certain limited seasons like *Calluna* (22, 23). Secondly, the majority of plants of this type grow very slowly and are hence unsuitable for culture work. Lastly, the rates of growth of a series of cuttings may show extreme variability, which makes it a matter of great difficulty to institute reliable comparisons of different treatments.

Preliminary investigations on a number of moorland plants, for which we are indebted to Miss V. M. Stansfield, indicated that *Eriophorum angustifolium* was the most suitable of the commoner moorland plants. Cuttings of this plant rooted readily, quickly and at all seasons, and their subsequent growth was less variable than was the case for other species. Seedlings, however, grew rather slowly and they were difficult to manipulate on account of their small size. Cuttings were therefore used as the normal material. The behaviour of *Eriophorum vaginatum* was closely similar to that of *E. angustifolium*, but it grew very much more slowly. In view of the still considerable variability in the cuttings, it was necessary to take precautions to ensure that the material used was as uniform as possible. To this end, the cuttings used were picked so that they had the same number of leaves, one rooting node, but no roots or externally visible new shoots. Dead leaves and sheathing leaf bases were removed and the cuttings were required to fall within narrow limits of weight. In this way similar groups of cuttings of known initial weight were prepared and these were placed in the culture solutions. Our normal practice was to employ twelve cuttings in each group, and of these, in most cases, at least ten were available for the final measurements. At the conclusion of the experiment, the fresh weight (after careful drying on filter paper) and dry weight (after heating to constant weight at 100° C.) were determined separately for the shoot and root of each cutting. From these weights the final dimensions of each cutting could be expressed as a percentage of its initial fresh weight. The mean percentage for the group of cuttings or the culture and the probable error of this mean were then calculated.

While the use of larger groups of cuttings would probably be desirable, it would appear that significant results can, with due precautions, be obtained

by the methods outlined in this paper. Apart from the care taken in obtaining uniformity in the cuttings, we attach considerable importance to the regular and frequent renewal of the culture medium (at least once a week). Further, in drawing conclusions, we have followed the usual practice of employing only those results where the differences between the means are more than three times the probable error (9). The records for *Eriophorum angustifolium* alone now include the results of growing over eleven hundred plants. It is important to note that all these results are in essential agreement and the reliability of our methods must be considered to be justified by this fact. In addition, the variability of the cuttings seems to be reduced to very small limits in observations undertaken to check this point. Four groups of ten cuttings selected in the usual way were grown in each of two solutions A 1 and A 2. The final dry weights of these groups of cuttings, expressed as percentages of their initial fresh weight, were:

Solution A 1	Solution A 2
50.1	45.2
51.6	44.7
48.4	43.5
49.1	45.0
Means 49.8	44.6

Probable errors based on the individual cuttings were not determined in this series. Check cultures of forty cuttings grown in solutions A 1 and A 2 at the same time gave very closely similar results, viz.:

Solution A, 50.6 Solution B, 45.4

The low variability and lack of overlapping results shown by the use of ten cuttings are substantiated by a similar series of observations on *Deschampsia flexuosa*, in which only five cuttings per culture were used. In this case, three cultures were grown in each of four solutions, and the results were:

Solution E	1	2	3	4
	39.7	54.5	42.0	23.8
	41.5	66.5	41.8	33.8
	39.3	54.0	40.5	28.2
Averages	40.2	58.3	41.4	28.6

The agreement between the results for any one solution is remarkable, considering the small numbers of cuttings in each culture.

Solutions. The solutions employed were various modifications of Shive's three-salt culture solution (27), containing potassium di-hydrogen phosphate, magnesium sulphate and calcium nitrate. The details of composition can be obtained from the Appendix, and they require no further reference here. The principles employed in the composition and rise of the culture solutions need further attention, however. The culture solutions were always dilute and they were replaced by fresh solution once a week. Rayner (22) has pointed out that the total concentration may be an important factor in the growth of

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Calluna cultures. All our cultures lie within or below the optimum concentration values 500–1000 p.p. mill. indicated by Rayner. We attach very great importance to the weekly changing of the culture solutions, since cultures in which solutions were left unchanged may give entirely different results.

Four types of solution were usually employed in a given experiment:

	I	II	III	IV
Calcium content	Low	Low	High	High
Basic ratio $\frac{K}{Ca}$	Low	High	Low	High

The calcium content of the solutions was approximately that of natural soil solutions or soil extracts (see p. 27)—“low calcium” being 10–20 p.p. mill. and “high calcium” 40–120 p.p. mill. The magnesium content was usually constant throughout a given series. Sodium hydroxide was added when necessary to obtain a required hydrogen-ion concentration, but the amount of sodium added never exceeded 1 p.p. mill. The alterations in the basic ratio were produced by variations in the potassium content, potassium di-hydrogen phosphate or potassium chloride being added to give a higher basic ratio. The value of this ratio was varied considerably in different experiments—but it was, in a given series, the same in solutions I and III, or in solutions II and IV. The calcium content of the solutions was increased by the addition of calcium nitrate, sulphate or chloride. Nitrates are supposed to be toxic to some heath plants, but we were unable to observe any harmful effects of this ion upon *Eriophorum*, even in far higher concentrations than those used in the experiments cited below.

The hydrogen-ion concentration of the solutions was controlled when necessary by the addition of hydrochloric acid or sodium hydroxide. It was checked colorimetrically (4) every three days, but usually had changed very little in a week. Most of the cultures were kept about pH 4.5—since this is about the average pH value of the soils or solutions in which *Eriophorum* grows naturally. Series of cultures at pH 5.8, 6.0 and 7.0 have also been used.

In order to keep some sort of a check on the change in the calcium content of the solution, the “hardness” of the solution was measured before and after the plants had grown in it. This was measured as the amount of standard oleic acid solution which had to be added to 20 c.c. of solution to obtain a permanent lather. Oleic acid forms insoluble soaps with both calcium and magnesium and hence the method measures the sum of the two metals present. The method was introduced in the first instance because of its rapidity—it being impossible to contemplate any extensive series of estimations by the usual oxalate method of estimating calcium (5) although the estimations of calcium given were made by this method. It was also thought that the growth of the plants might show some connection with the power of the solutions to form insoluble soaps which is directly estimated by the hardness method. Further, if this had proved to be the case, the hardness of solutions from soil,

etc., could be readily estimated in the field. In practice, however, the determinations of hardness proved to be of little value and, except for a few isolated references in the text, they are not included.

EXPERIMENTAL RESULTS

In order to obtain coherence in the presentation of the experimental data, we propose to consider them under the following headings: (1) calcium effects, (2) basic ratio effects, (3) anatomical details, (4) magnesium effects, (5) acidity effects, (6) germination, (7) climatic factors, (8) natural and edaphic factors. Each of these sections really enlarges on the first and is necessary to the full consideration of the calcium effect as shown in our cultures.

(1) CALCIUM EFFECTS.

The nature of the principal differences produced in *Eriophorum angustifolium* by varying the proportion of calcium in the rooting medium can be estimated from the results given in the following tables.

Table I. *Final dry weight of cuttings as a percentage of their initial fresh weight, after twelve weeks.*

Solutions A 1 and A 2, pH 4.6, basic ratio 3. (80 plants per culture.)

Calcium content p.p. mill.	20	40
Total dry weight	49.80	44.61
Roots—dry weight	2.94	2.09
Fresh weight of tops	4.46	4.15
Dry weight		

Probable errors not determined (see p. 3).

Table II. *Final dry weight as percentage of initial fresh weight.*

Solution B, with increasing proportions of calcium as sulphate; pH 4.6, ten plants per culture, sixteen weeks. (Series C.)

Calcium content p.p. mill.	10	50	200
Basic ratio	2.0	0.4	0.08
Total dry weight	69.7 ± 1.7	71.2 ± 2.2	53.3 ± 1.6
Roots—dry weight	9.07 ± 0.40	13.8 ± 0.34	5.2 ± 0.51
Fresh weight of tops	4.46 ± 0.044	4.19 ± 0.045	4.20 ± 0.039
Dry weight			

It appears from these results that increased proportions of calcium may lead to decreased production in final fresh weight, dry weight and root weight. There is also a pronounced tendency for the water content of the cuttings to be lower, as shown by the ratio of fresh weight to dry weight $\left(\frac{\text{fresh weight}}{\text{dry weight}}\right)$. It is to be noticed also that in our experience, the best calcium content of the solution is about 12 to 20 p.p. mill. at pH 4.5. The following results from the growth of cuttings in the same solution diluted to various degrees, may serve to illustrate this point as well as the effect of dilution.

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Table III. *Dry weight yield in solutions of different concentrations.*

Solution C, pH 4.6, basic ratio 1.7, sixteen weeks, twelve plants.				
Culture concentration	1	0.5	0.2	0.05
Calcium content p.p. mill.	60	30	12	3
Final dry weight*	65.5 ± 1.22	71.1 ± 0.35	80.3 ± 1.67	57.6 ± 1.72

* As percentage of initial fresh weight.

It is evident that *Eriophorum angustifolium* requires calcium, although it will normally grow well in solutions of low calcium concentration. We would, in addition, emphasise a point, to be considered in detail at a later stage, that the calcium effects are variable and are not always of similar intensity even in solutions of closely similar composition.

(2) EFFECTS OF BASIC RATIO.

The effects of calcium depend not only upon the calcium content of the rooting medium but also to some extent upon the proportion of potassium and sodium this medium contains. When this proportion, the *basic ratio* $\left(\frac{K + Na}{Ca}\right)$ is high, the effects of calcium *may* be reduced. It has proved very difficult to assess the exact value of the basic ratio because its effect undoubtedly varies in response to other factors both in the solution and the external environment. Bearing in mind the fact that increased calcium may produce (1) a beneficial effect when the calcium content of the solution is very low (10 p.p. mill. or less), or (2) a harmful effect when the calcium content of the solution exceeds about 30 p.p. mill., we shall, at least, have to consider the effect of the basic ratio in solutions of both types.

The inability of *Eriophorum* to grow well in solutions of very low calcium content is largely removed by increasing the basic ratio.

Table IV. *Yield in solutions containing 10 p.p. mill. of calcium pH 4.5.*

	Solutions D 1 and D 2	
Basic ratio	1.5	0.5
Total dry weight*	55.5 ± 1.2	32.1 ± 1.6
Dry weight—roots*	4.7 ± 0.11	0.74 ± 0.04
Fresh weight		
Dry weight of tops	4.16 ± 0.14	4.25 ± 0.17
Reduction in hardness of solution	1.8	0.36

* As percentage of initial fresh weight.

It would appear from this result that an increased basic ratio may cause an increase in the amount of calcium absorbed and hence an increase in yield. This supposition is also supported by the figures for the reduction in the hardness of the solution—which are given as c.c. of standard soap solution per week—on the average for four weeks. The hardness is reduced more in the solutions of higher basic ratio and hence more calcium and magnesium were absorbed from these solutions. It is possible that the increased basic

ratio may increase the permeability of the tissue, permitting more rapid entry of calcium. On the other hand, the general assumption is, that higher proportions of potassium or sodium reduce the rate of entry of calcium ions (25) though possibly this may not apply in solutions of very low concentration. It should be noticed in this connection, therefore, that the effect of a high basic ratio in increasing calcium absorption apparently tends to disappear in solutions of higher calcium content. The following figures illustrate this.

Average weekly reduction in hardness of solution (as c.c. of standard soap solution).

	Basic ratio	
Calcium content	High (1·5)	Low (0·5)
15 p.p. mill.	1·4	0·5
50 p.p. mill.	3·05	2·9

Along with this apparent similarity in the amounts of calcium absorbed in the solutions of higher calcium content but different basic ratio, we have the tendency for the beneficial effect of a high basic ratio to disappear as the calcium content of the solution increases. This, as well as the general effects of a high basic ratio, can be estimated from Table V, which gives data for three species.

Table V. *Effect of solutions of different basic ratio and calcium content. Solution E.*

Basic ratio	Total dry weight*		Root—dry weight*		Fresh weight Dry weight		Calcium content p.p. mill.
	4	2	4	2	4	2	
<i>Eriophorum angustifolium</i> }	39·5 ± 0·91	33·1 ± 0·49	1·22 ± 0·093	0·70 ± 0·04	3·81 ± 0·075	3·49 ± 0·12	20
pH 5·8	34·2 ± 0·93	32·5 ± 1·02	0·48 ± 0·066	0·54 ± 0·06	3·21 ± 0·086	3·35 ± 0·07	40
<i>Eriophorum vaginatum</i> }	31·4 ± 1·17	20·7 ± 1·43	2·2 ± 0·058	0·8 ± 0·071	7·1 ± 0·18	4·8 ± 0·18	20
pH 4·8	23·1 ± 1·46	24·5 ± 0·98	1·5 ± 0·069	1·0 ± 0·046	6·9 ± 0·21	5·1 ± 0·16	40
<i>Deschampsia flexuosa</i> }	58·3 ± 2·07	40·2 ± 0·32	10·6 ± 0·33	3·2 ± 0·07	3·02 ± 0·039	2·97 ± 0·03	20
pH 4·8	28·6 ± 1·58	41·4 ± 0·26	2·4 ± 0·14	3·6 ± 0·10	2·57 ± 0·07	2·35 ± 0·032	40

* As percentage of initial fresh weight.

In these results, highest total yield, root yield and water content are found consistently in the solution of low calcium content and high basic ratio. (It should be noticed that the data for *Eriophorum angustifolium* are not exactly comparable with those previously discussed, as they were carried out in less acid solutions.) It is, further, of interest to observe that, under the conditions of this experiment, the water content of *Eriophorum vaginatum* apparently depends more on the basic ratio, while the water content of *Deschampsia flexuosa* is more closely dependent on the calcium content. While, in all the results, there is rough correlation between high water content and high yield,

it is equally clear that high water content does not necessarily mean high yield, although it will undoubtedly be one of the favourable factors. The effect produced by calcium and the basic ratio upon the water relations is clearly one of importance. Two factors seem to operate in producing high water content in solutions of low calcium content and high basic ratio. Increased root production will, on the whole, favour the production of high water content, but it seems clear from an examination of Table V that high water content may occur along with small roots—notably in the case of *Deschampsia*. The other factor modifying the water content is the rate of transpiration. Both Reed (24) and Hansteen-Cranner (11), working with solutions of single pure salts, have found that calcium produced an increased rate of transpiration, while potassium and sodium caused a reduced rate. This would clearly tend to give a higher water content in plants grown in solutions rich in potassium or sodium salts, and in this respect our results are explained by those of Reed and Hansteen-Cranner. Further, in a few cases we have estimated the amount of water absorbed from our solutions, which gives a rough guide to the amounts transpired. In general, there is a rather higher rate of transpiration in solutions rich in calcium, although, in view of the doubtful accuracy of the method, we should hesitate to call this significant without the evidence of the authors cited. Our limited results do suggest, however, that significant differences in the ratio of fresh weight to dry weight are associated with differences in transpiration rate.

The following data were obtained by growing cuttings in the solutions for two months in the usual way, and then leaving the solutions unchanged for a month to allow the measurement of the water absorbed by the plants.

Table VI.

Solutions D	1	2	3	4
Calcium content	12	12	48	48
Basic ratio	1.5	0.5	1.5	0.5
Fresh weight				
of tops	4.63	4.41	4.38	3.96
Dry weight				
Transpiration, c.c.*	20.1	20.9	20.9	24.2

* As c.c. of water absorbed per gram of final fresh weight of tops.

It will be noticed that the water content is inversely proportional to the amount of water transpired. The position is, therefore, that the effects of calcium and the basic ratio upon the water relations seem to be largely due to alterations in the rate of transpiration. We have also to remember that the beneficial effect upon yield of a high basic ratio operates chiefly in solutions of low calcium content, and further, that alterations in the water relations are not always associated with alterations in yield.

(3) ANATOMICAL CHARACTERS ASSOCIATED WITH CALCIUM AND BASIC RATIO EFFECTS.

In addition to the effect produced on weight and water content, solutions rich in calcium may also produce distinct differences in root size and morphology. The extremes observed have always occurred on contrasting roots from

solutions poor in calcium with a high basic ratio, with roots of similar age from solutions of low basic ratio, and high calcium content, as, for example, in the plants described in Table V. In the more calcareous solutions some or all of the following changes may be seen: (1) scarcity of root hairs, (2) failure in lateral root development, (3) pink or brown coloration. In extreme cases the lateral roots cease developing as soon as they emerge from the cortex of the main root, so that they are visible only as brown protuberances on the surface. In such a case as this, the failure of the lateral meristems to develop is associated with the almost complete differentiation of the cells of the root apex, and only about one or two layers of cells near the outside of the root remain non-vacuolated and apparently meristematic. Thus solutions rich in calcium appear to favour rapid vacuolation of the dividing cells. Along with this difference in the meristems, there are modifications of the cell walls of the mature roots. The walls of the cortex are usually noticeably thinner in the solutions of higher calcium content, and the exodermis is also thinner—often only one cell thick and usually interrupted by thin-walled cells whose walls give no fat stains (Sudan III or osmic acid). In such solutions there is also a decided tendency for fatty material to appear as globules, either on the exodermis walls or on those of the central conducting strand.

In solutions of low calcium content, the walls of the cortical cells are thicker, and they show little stratification and often have a gelatinous appearance. The exodermis is usually continuous and two or three cells in depth. We are inclined to attribute some importance to these apparent differences in wall composition. A curious feature of the roots examined from solutions of high calcium content is that lateral roots often grow down through the cortex. It seems as though, under these conditions, the exodermis may be so resistant that the root initials cannot penetrate it. If they do, their development is usually retarded, but otherwise they may grow down between the exodermis and endodermis of the parent plant. This feature has not been observed in solutions of low calcium content and high basic ratio and, if the suggested explanation is correct, it agrees with the observation that the cortical cell walls of roots from such solutions are thicker and more gelatinous in appearance, and, hence, presumably softer.

Another noteworthy feature observed in the cultures of all three species described in Table V, as well as in other cultures, is that the solution of low calcium content and high basic ratio may become slightly turbid and opalescent during the period of rapid root development. In *Deschampsia flexuosa* only, this turbidity was also accompanied by a swollen and gelatinous appearance in the roots just behind the growing point. Hansteen-Cranner (11) has observed similar changes during the growth of Lupin seedlings in solutions of single sodium or potassium salts, and they are apparently caused by the diffusion of the soluble potassium or sodium salts of fatty acids from the cell walls into the outer solution. In the presence of suitable quantities of

calcium, insoluble calcium salts of these substances are apparently formed and precipitated in the wall, giving it greater rigidity—for the loss of these substances as soluble salts leaves the walls soft and gelatinous.

It seems probable that these wall differences find another expression in the fact that the root hairs of *Eriophorum* tend to be longer and more abundant in solutions of low calcium content and high basic ratio. If the walls are softer and more gelatinous under these conditions, then they will be more readily stretched during the period of cell extension—so that longer and more abundant root hairs should result. Hansteen-Cranner's work (11, 12) thus seems to provide a clue to the three main facts observed in connection with root structure and development. It seems that we can associate with low calcium content and a high proportion of potassium (1) diffusion of material from the roots (and swelling in *Deschampsia flexuosa*), (2) the thick and gelatinous character of the cell wall as revealed by hair formation and by microscopical examination; while high calcium, on the contrary, is associated with (3) the frequent inability of the lateral roots to pierce the outer layers of the cortex. So far as the physical character of the cell walls can be estimated, therefore, high calcium gives thinner, less gelatinous and more resistant cell walls.

Influence of the cell wall on the water relations.

These characters are probably of importance in providing a clue to the differences in water content shown by the aerial parts of the plants. Owing to the difficulties of measurement, it has not proved possible to observe significant differences in the thinner cell walls of the leaves, although it seems extremely probable that similar, though perhaps less marked, differences in their composition must exist. If so, they would affect the rate of transpiration (and hence the water content), since this must depend upon the chemical and physical character of the evaporating surface—the cell wall. Indeed, Hansteen-Cranner's investigations already cited (12) suggest that this is a fundamental factor, for his evidence permits the assumption that the greater transpiring power of plants grown in solutions of calcium salts is due to the presence of calcium salts of fatty substances in the cell walls. In the presence of such substances, cellulose membranes absorb water less rapidly than do similar membranes impregnated with sodium or potassium salts, which act in the reverse way.

If the water relations of plants can be affected in this way by the cell wall composition, then we might expect that this effect would be more pronounced either when the cell walls are thick or when their fatty constituents are present in considerable proportions. The thickness of the cell walls appears to be a very noticeable feature of the anatomy of the two species of *Eriophorum* examined, and this would, therefore, suggest the importance of the wall effect in controlling their water relations. Priestley and Hinchliffe (18, 19) have already drawn attention to the considerable proportions of fatty materials

present in *Eriophorum*, in common with other moorland plants, as shown in the peculiar features of their anatomy. This, also, therefore, suggests that the cell wall effect is of considerable importance.

(4) THE EFFECT OF MAGNESIUM.

According to Hansteen-Cranner's observations with solutions of pure single salts, magnesium affects the water relations of plants in a similar manner to potassium and sodium, a fact which this author attributes to the ability of magnesium to form soluble salts with the fatty materials of the cell wall. It is necessary to point out that magnesium only forms soluble salts with a limited number of fatty acids, and in a large number, perhaps the majority, of cases, the magnesium soaps are relatively insoluble and more like those of calcium. It is possible because of this or from some similar cause that the behaviour of magnesium in reference to the growth of *Eriophorum* has proved very difficult to define. In only three cases has a high proportion of magnesium produced any appreciable effect. In two of these the effect resembled that of calcium, but in the other case the effect was one normally produced by higher proportions of potassium. The most striking effect was produced in a set of cultures in which three solutions were used containing K, Mg and Ca in the following proportions (as p.p. mill.):

	Solution I "Low Mg"	Solution II "High Mg"	Solution III "High Ca"
K (as KH_2PO_4)	120	80	120
Mg (as MgSO_4)	4	40	4
Ca (as $\text{Ca}(\text{NO}_3)_2$)	20	20	40

Solutions I and II were each set up at two pH values, pH 4.5 and 6.0, while solution III was set up in duplicate. The percentage yields obtained in these cultures were as follows:

	Low Mg	High Mg	High Ca
pH 4.5	64.2 ± 0.86	59.5 ± 0.69	$56.8 \pm 0.75, 57.5 \pm 0.72$
pH 6.0	58.6 ± 0.70	51.2 ± 0.75	---

It is noticeable that the effect of magnesium in these cultures is precisely the same as that of calcium—it produces a marked reduction in dry weight. In a subsequent culture this result was confirmed, so that it is probably safe to assume that calcium and magnesium may have closely similar effects upon the dry weight yield. On the other hand, one very striking feature of the "high magnesium" cultures was the length and number of the root hairs—a feature usually associated with a high proportion of potassium in our observations. Since we attribute this marked root hair production to the gelatinous nature of the cell walls, it seems that in this respect magnesium produces effects akin to those ascribed to it by Hansteen-Cranner and hence opposed to those produced by calcium. In any cultures in which transpiration has been measured high magnesium apparently tends to produce a small reduction in the

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transpiration rate. This may or may not be significant, but it suggests a possible similarity to potassium in this respect also.

(5) EFFECTS OF ACIDITY.

In the succeeding paragraphs, the problem to be examined is the effect of the hydrogen-ion concentration of the rooting medium upon the behaviour of *Eriophorum angustifolium* in relation to calcium. The growth of cuttings in solutions containing 15 p.p. mill. of calcium was examined in a series of cultures of which the pH values varied between pH 2 and pH 9. No growth took place in cultures of these extreme pH values, but between pH 3 and pH 8 the following data were obtained.

Table VII.

	Solution F.					
pH	3	4	5	6	7	8
Final dry weight*	36.5 ± 2.8	93 ± 6.6	108 ± 6.1	107.5 ± 6.0	93.5 ± 5.7	44 ± 3.2
Roots—dry weight*	0.8	6.5 ± 0.4	5.2 ± 0.37	10.3 ± 1.4	2.6 ± 0.17	3.0 ± 0.21

* As percentage of initial fresh weight.

Allowing for the size of the probable error, it is clear that no great difference in growth took place between pH 4 and pH 7, limits which represent approximately the observed range in which this plant grows in nature. Root production at pH 7.0 was, however, significantly smaller and the roots were less branched, in a way which rather suggested the effects of high calcium. The figures for water content were rather variable and consequently significant data were not obtained. In a subsequent series, however, the following figures were obtained, using solution B 1, which contains 20 p.p. mill. of calcium.

Table VIII.

pH	4	5	6	7
Final dry weight*	40.5 ± 1.10	40.2 ± 1.13	42.5 ± 1.24	33.6 ± 1.02
Roots—dry weight*	1.45 ± 0.13	1.23 ± 0.11	1.38 ± 0.12	0.49 ± 0.07
Fresh weight of tops*	4.72 ± 0.07	4.90 ± 0.08	4.76 ± 0.07	4.32 ± 0.10

* As percentage of initial fresh weight.

Here, again, the figures obtained at pH 4, 5 and 6 were closely similar, but at pH 7 there is marked reduction in yield (total and roots) and also in water content. It is suggestive to notice that this effect is rather more pronounced in solutions of higher calcium content, and it seems to be due to the more rapid absorption of calcium at pH 7 as compared with pH 4.5. Thus, the amounts of calcium absorbed by plants of closely similar size and root development in solutions of pH 4.5 and 7.0 were as follows:

Calcium absorbed per gram of dry weight per month.

Calcium in solution	15 p.p. mill.	50 p.p. mill.
pH 4.5	4.2 mgm.	8.2 mgm.
pH 7.0	6.1 „	13.2 „

Thus, the absorption of calcium was 50 per cent. greater at pH 7 as compared with that at pH 4.5. Arrhenius (1) and Theron (31) have obtained similar results for wheat and cucumber respectively, and the routine estimations of "hardness" in our cultures confirm the above result. In a set of cultures, to which reference has already been made, the dry weight yields (as percentages of the initial fresh weight) were:

	"Low Magnesium" 20 p.p. mill. calcium	"High Magnesium" 20 p.p. mill. calcium	40 p.p. mill. calcium
pH 4.5	64.2	59.5	56.8 and 57.5
pH 6.0	58.6	51.2	—

The effect of higher pH value was here similar to that of higher calcium both on the total yield and also on the root form and weight. Parallel to this is the fact that the hardness was reduced more at pH 6 than at pH 4.5.

Average weekly reduction in hardness of culture solutions during five weeks.

			Initial hardness	Final hardness	Difference
		pH	c.c.	c.c.	c.c.
1	“Low Magnesium” (calcium low)	4.5	15.6	13.7	1.9
2		6.0	15.6	12.5	3.1
3	“High Magnesium” (calcium low)	4.5	24.3	22.4	1.9
4		6.0	24.3	19.0	5.3
5	High calcium	4.5	22.0	18.6	3.4

These figures roughly indicate the relative amounts of calcium and magnesium absorbed, and from them we can calculate the relative absorption of calcium and magnesium for solutions 1-5 expressed as mgms. of calcium per gm. of dry weight of plant per week, viz. (1) 1.9, (2) 3.0, (3) 2.2, (4) 4.4, (5) 3.2. Roughly these figures for the relative calcium absorption will be found to be inversely proportional to the yield. It may be assumed, therefore, that a higher pH value will be associated with more rapid absorption of calcium and it should, therefore, follow that the effects of a given concentration of calcium will be accentuated at pH 6 or 7 as compared with pH 4.5, the usual reaction of our culture solutions.

We have available the following data for *Eriophorum angustifolium* grown in similar solutions (B 1) whose calcium contents were varied by the addition of CaSO_4 (cultures of ten plants).

Dry weight of cuttings.

(As percentage of initial fresh weight.)

Ca content p.p. mill.	12	90	360
(a) pH 4.5	36.6	32.1	25.3
(b) " 4.5	34.5	33.5	29.5
(c) " 4.5	—	32.7	21.5
(d) " 7.0	35.0	28.0	16.6
(e) " 7.0	—	28.1	20.0

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Taking the average result for each calcium content at each pH and expressing these as percentages of the average yield in solutions containing 12 p.p. mill. of calcium, we get the following relative yields at the different hydrogen-ion concentrations:

Ca content p.p. mill.	12	90	360
pH 4.5	100	92.5	71.5
pH 7.0	100	80	52.3

showing that the effect of high calcium is greatly accentuated by a high pH value.

We come next to the question of the effect of the basic ratio at different pH values. This is illustrated by the following series of results:

Table IX. *Dry weight of cuttings (as per cent. of initial fresh weight) at different pH values, calcium contents and basic ratios.*

Series H.				
Solution D	I	II	III	IV
Calcium p.p. mill.	12	12	48	48
Basic ratio	1.5	0.5	1.5	0.5
pH 4.5	57.5	33.3	80.8	59.1
pH 7.0	67.0	39.6	57.4	58.0
Fresh weight of tops in the above solutions.				
	Dry weight			
pH 4.5	4.25	4.34	4.32	4.44
pH 7.0	4.63	4.41	4.38	3.96
Transpiration to nearest c.c. per gm. of fresh weight per month.				
pH 4.5	21	22	21	22
pH 7.0	20	21	21	24
Calcium absorbed—mgm. per gm. of dry weight per month.				
pH 4.5	4.2	—	8.2	—
pH 7.0	6.1	—	13.2	—

In this series the individual weighings of cuttings were omitted in order to allow of measurements of transpiration and calcium absorption. Probable errors cannot be given, therefore, but the cuttings were very uniform in each solution. The results indicate that the effect of the basic ratio on *yield* decreases as the calcium absorption increases, so that it is largest in solutions of 10 p.p. mill. Ca at pH 4.5 and negligible in solutions with high calcium content at pH 7.

Comparing the quantities of calcium absorbed with the relative effect of the basic ratio on yield—expressed as yield in high basic ratio (H) over yield in low basic ratio (L)—we get:

Solutions	pH	Calcium absorbed	High Low
I and II	4.5	4.2	1.73
	7.0	6.1	1.69
III and IV	4.5	8.2	1.37
	7.0	13.2	0.99

This is clearly equivalent to a former conclusion (p. 7) that the effect of the basic ratio on yield is more marked in solutions of low calcium content.

On the other hand, the effect of the basic ratio on the *water relations* is only clearly shown in the solutions of high *pH* value and calcium content, under the conditions of this experiment. This seems to emphasise the point, to which reference has previously been made, that the two effects (on yield and water relations) are not necessarily very closely related. Two further points of interest are indicated in this table. In the first place, a similar low yield is produced both by too little calcium absorption (solution I at *pH* 4.5) or by too much (solution III at *pH* 7). The greatest yields are associated with intermediate quantities of available calcium. Secondly, the "optimum" hydrogen-ion concentration for the growth of *Eriophorum* may vary with the composition of the nutrient medium. It is at higher *pH* values in solutions of low calcium content, but at lower *pH* values if the calcium content of the solution is high.

The essential points, then, which emerge from this consideration of the effects of acidity are (1) that calcium absorption increases as the acidity of the solution decreases, (2) that the optimum hydrogen-ion concentration for the growth of *Eriophorum* may vary with the calcium content and basic ratio of the solution, (3) that the effect of the basic ratio upon yield appears to decrease with decreasing acidity but the effect on water relations may be more clearly marked in less acid solutions.

GERMINATION OF *ERIOPHORUM*.

It was originally intended to try to carry out a set of cultures in which seedlings were raised from seeds to maturity, but the seeds of *Eriophorum angustifolium* germinated rather slowly and the seedlings were delicate and not easily handled, so that progress proved to be rather limited. Some interesting data were acquired, however, for which we are indebted to Miss V. M. Stansfield, and to these a brief reference is desirable. The solutions used were similar (B 1) but contained different proportions of calcium as sulphate (10 and 60 p.p. mill.). In each series, fifty seeds were allowed to germinate on damp filter paper moistened daily with the culture solutions and kept in a warm and moist chamber. We give below the percentages of germination of these seeds (1) after four days, and (2) finally.

Percentage germination of Eriophorum angustifolium.

Calcium content of solution		Four days		Total	
		Low	High	Low	High
Expt. 1	<i>pH</i> 4.5	28; 25	30	58; 68	58
" 2	" 4.5	40; 36	48	70; 80	74
" 3	" 4.5	12	22	56	56
" 4	" 7	57	31	82	76
" 5	" 7	59	37	78	72
Average	" 4.5	28	33	66	63
"	" 7	58	34	80	74

Now these results show considerable variability from one experiment to the next, so much so, that when they were originally carried out, no importance

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was attached to the differences in percentage germination, especially as the final results show but little difference in the germination in the two different solutions. In the light of our subsequent knowledge of the effect of acidity on calcium absorption, it is of great interest to observe that in acid media (*pH* 4·5) the most *rapid* germination takes place in solutions relatively rich in calcium, while in neutral solutions (*pH* 7) germination is most rapid in solutions containing smaller quantities of calcium. The subsequent history of the seedlings agrees with this conclusion. The seedlings grown under conditions favouring rapid germination developed best. The best of the four solutions for seedling culture was undoubtedly solution I (low calcium) at *pH* 7, while plants grown in the neutral solutions generally remained larger and healthier than those in the acid solutions. These cultures had finally to be discontinued on account of the slowness of development of the seedlings.

(7) CLIMATIC INFLUENCES.

The possible importance of climate as a factor in the operation of the calcium effect naturally received some consideration when it was realised that the water relations of the plants might be an important feature of the whole problem. While it was obvious that dry atmospheric conditions might easily determine whether or not the drying effect due to high calcium was obtained, the realisation of the importance of the climatic factor sprang from a series of observations made during the winter of 1924. In order to continue the investigations through the winter, it had been our practice to make use of a small laboratory continuously lit by electric light, which was readily maintained at a fairly constant temperature. In this room most plants, including *Eriophorum*, make abundant growth, and hence confirmatory series of cultures could be carried on through the winter. In the particular series (D) under consideration, although we were using solutions which had previously proved successful, no significant calcium effect was obtained. Not only were the plants strikingly similar in appearance, but their roots were, if anything, more branched and the water content also proved to be higher in "high calcium."

Table X.

Solution G	Series D.			
	1	2	3	4
Ca content p.p. mill.	20	20	40	40
Basic ratio	3	6	3	6
Dry weight %	65·3 ± 1·19	64·2 ± 0·86	56·8 ± 0·75	60·9 ± 0·81
Roots—dry weight	4·65 ± 0·21	3·90 ± 0·30	4·71 ± 0·19	4·68 ± 0·22
Fresh weight				
Dry weight	5·40 ± 0·10	5·19 ± 0·061	5·99 ± 0·06	6·08 ± 0·072

Solution; *pH* 4·5; 9 weeks.

A rigorous examination of the conditions under which the experiment had been carried out suggested that it differed from the previous successful experiments which had been staged in a cool greenhouse, chiefly in the high tem-

perature at which this winter series had been kept, possibly also in the high atmospheric humidity of the winter culture room.

The cultures had been constantly kept in air temperatures of 21°–27° C., with their roots in solutions at 18–20° C. The experiments were, therefore, repeated, using similar cultures but keeping the air temperatures down to 12–15° C. and the solutions at 7–10° C. The relative humidity of the atmosphere was closely similar in both experiments. Under these conditions, the results in twelve weeks were:

Table XI.

Solution G	Series E.			
	1	2	3	4
Ca p.p. mill.	20	20	40	40
Basic ratio	3	6	3	6
Total dry weight*	35.4 ± 0.31	35.7 ± 1.26	31.7 ± 0.67	33.0 ± 0.57
Roots—dry weight*	1.47 ± 0.11	1.57 ± 0.14	0.90 ± 0.08	0.86 ± 0.05
Fresh weight of tops*	4.01 ± 0.040	4.33 ± 0.053	3.98 ± 0.066	4.03 ± 0.051
Dry weight				

* As percentage of the initial fresh weight.

The most noticeable difference in this series was in root production, which showed a marked calcium effect in reduced size and branching coupled with a just significant difference in dry weight. Equally important was the reduction in the water content of all the cultures, as compared with the previous set, while the maximum water content appeared in the usual place in this type of culture, viz. in high basic ratio and low calcium content. A curious feature was that the basic ratio apparently produced little alteration in yield, although it affected the water contents in low calcium. The general conclusion to be drawn from this experiment is that the calcium effects can be very greatly reduced by the employment of high temperatures. The data show that this reduction was not due to the exhaustion of the calcium in the solutions, since the hardness of these solutions was rarely reduced by more than 10 per cent. in a week, and never by more than 20 per cent. Hence the majority of the calcium remained in the solution. The temperature effect is therefore some metabolic effect, which either alters the way in which the calcium is utilised internally or else makes the plant less sensitive to the calcium effects. We suggest that both factors may be in operation. Attention has already been drawn to the probable importance of the cell wall composition as a factor in producing calcium effects, and our observations have agreed with those of Hansteen-Cranner in indicating the importance of calcium soaps in this connection.

According to Lewkowitsch (14), the solubility of the calcium soaps is extremely sensitive to changes of temperature, so that, although their solubility is very low at normal temperatures, a small rise of temperature is sufficient to produce a relatively considerable change in solubility. If we apply this conclusion to the question of the deposition of Ca soaps in the cell wall, then it would follow that a rise of temperature would slow down this process

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very considerably, since the calcium soaps would be relatively much less easily precipitated. The effect of calcium upon root structure and the water relations of *Eriophorum* is clearly very largely dependent upon the precipitation of Ca soaps in the cell wall. Hence a rise of temperature, by considerably reducing the rate of precipitation, might considerably reduce the calcium effect, particularly the effect of calcium upon the roots and the water relations.

So far as the temperature affects the metabolism of plants, it appears (Tottingham, 32) that a higher temperature increases the rate of nitrogenous metabolism more rapidly than it affects alternative types (of synthesis). Hence the proportion of organic nitrogen compounds in the plant is higher than is normal. Unpublished work in this laboratory has shown that this condition of "high nitrogen" may give rise to higher water content in the plant. High temperatures are, therefore, indirectly followed by higher water contents, and the more favourable water relations thus induced would clearly tend to counteract the drying effect of high calcium.

The rôles of temperature and calcium in the water economy are, of course, capable of being modified by the usual atmospheric factors which affect transpiration. While it is not possible to describe the atmospheric conditions of our culture chambers very precisely, yet we can contrast three sets of cultures in the high temperature chamber used in winter, in which the humidity varied considerably while the temperature remained fairly constant. The most humid conditions employed were those of the exceptional experiment to which reference has already been made (Table X). During the course of this experiment, the usual procedure was to water the floor of the chamber heavily twice a day. The normal procedure, a single daily watering, was employed in numerous other experiments of type F, G (below), while, for a few of the earliest cultures in this room, watering was not employed (C). While no continuous records of atmospheric humidity exist, the available data as to the readings of wet and dry bulb thermometers agree with the estimate of humidity given above. Data for greenhouse cultures show similar but much smaller variations in humidity, as summarised below. The ratio of fresh weight to dry weight given in this summary represents the average of all plants in the series of cultures.

Table XII.

Culture series	Number of plants	Fresh weight Dry weight	Approximate solution temperature	Remarks
D	72	5.94	18-22° C.	Room heavily watered (Table X)
E	50	4.08	7-11	Low temperature series (Table XI)
F	20	4.81	17-20	Room watered moderately (Table VIII)
G	40	4.68	17-20	" " " "
C	36	4.28	17-20	Room occasionally watered (Table II)
A	48	3.46	11-15	Dry greenhouse (Table V)
B	48	3.32	11-15	" " "
L	40	4.38	16-20	Moist " (Table IX)
H	80	4.34	16-20	" " "

In the above table, series F, B and L are given as checks on other series which have been given in detail elsewhere. The figures indicate quite definitely that the water contents of the plants can be controlled by varying the humidity of the atmosphere, as well as by altering the temperature. We have emphasised, in this connection, the cultures grown under controlled conditions of light, simply because estimates of atmospheric humidity were also available; but the relation of water content to humidity is clearly visible in our other cultures, as, for example, A, B, L and H, for which consistent differences in humidity are recorded. Now, it has been noted that the calcium effect disappears in series D with high water content, while in series A and B it was very well marked when water content was least. Is it possible to estimate the relative magnitude of the calcium effect in relation to the fresh weight/dry weight ratio?

In order to attempt this it will be necessary to confine the discussion to solutions having similar composition and calcium contents, of which we have D, E, X and A (solution G), which give a large range of water contents. The roots will presumably be most affected by the composition of the solution, since they are in contact with it, so that relative root yield in solutions of high and low calcium content may be taken as one test of the calcium effect. We shall express the *relative root yield* as the maximum percentage increase of root yield per week in low calcium solutions, as compared with high calcium solutions.

Series	Fresh weight Dry weight	Maximum root yield in solutions of low Ca*	Minimum root yield in solutions of high Ca(H)	Difference* (D)	D as % of H
A	3.54	0.094	0.037	0.057	154
E	4.08	0.127	0.072	0.055	76
X	4.65	0.171	0.150	0.021	14
D	5.94	0.517	0.520	—	0

* Dry weight yield of roots per week as a percentage of the initial fresh weight of cuttings.

The figures obtained by this method are, of course, only approximate, but they support the assumption that the difference in root yield between similar solutions of high and low calcium decreases as the water content of the plants increases. In agreement with this is the fact that calcium effects have, in our cultures, been slight or negligible when the fresh weight/dry weight ratio exceeded 4.4 or 4.5, unless considerably higher calcium concentrations were employed than normally. It appears justifiable to assume, therefore, that the calcium effect on root yield is a variable, depending on the physiological humidity of the environment. We incline, also, to the belief that the calcium and basic ratio effects on the water relations may also vary with the water content of the plants. This possibility is indicated by the consideration of the examples taken above. In A and E (pp. 7 and 17) high water content only occurred in low calcium and high basic ratio, while in D and X (p. 16) little

difference was observed in the water contents or those in high calcium were somewhat higher. Similarly, in series H (p. 14), low water content only occurred in solutions of high calcium content, low basic ratio and high pH. The indications suggest, therefore, that, as the water content of the plants increases, the drying effects of high calcium concentrations become increasingly difficult to produce.

The analysis attempted above leads to the recognition of the fact that the water content of *Eriophorum angustifolium* can undoubtedly be controlled by altering the temperature and humidity of the atmosphere, and that conditions that lead to high internal humidity also lead to a reduction or disappearance of the calcium effects. Considerable importance is attached to these facts because, not only do they serve to account for the marked degree of variation in the intensity of the calcium effects observed in our cultures, but also because they seem to have a direct bearing upon the results and interpretation of the field experiments to be described next.

(8) NATURAL HABITAT FACTORS.

It is now necessary to indicate the conditions under which *Eriophorum* grows in nature and to see if these bear any resemblance to those which have operated in the case of the laboratory cultures. The most complete observations are those from Austwick Moss, in West Yorkshire. This "moss" is a typical area of "lowland moor" as described by Rankin (20). It is dominated in the centre by *Eriophorum angustifolium* and *E. vaginatum*, the former occurring in extensive water-logged depressions, which are usually old peat cuttings. This area merges through a transitional and drier zone, with abundant *Calluna*, into a region on the north side, in which *Molinia coerulea* is dominant, while *Juncus sylvaticus*, *Myrica gale*, *Phragmites communis* and *Salix cinerea* are abundant or locally subdominant. This zone is associated with the flushing effect of a small stream, and it will be referred to as "fen" (cf. 15). In both the *Eriophorum* bog and the "fen" zone the water table is normally at or near the surface, and it is an easy matter to collect water from each zone, to analyse these samples and to determine their effect upon the growth of *Eriophorum*.

	pH	Calcium p.p. mill.	Potassium and sodium p.p. mill.
<i>Eriophorum</i>			
Bog water	4.5	10	11
Fen water	5.8	34	14

Both the solutions were peaty, the fen water being of the light golden brown colour usually associated with oxidised peat. The bog water has never yet shown the presence of nitrates, but these are usually present in some quantity in the fen water. So far as the growth of *Eriophorum* is concerned, the calcium content of the bog water would appear to be rather below the best values as found in the laboratory experiments, while the fen water has a

calcium content that approaches that of some of the "high calcium" solutions employed. The basic ratios are similar to those of some of our experiments, but rather lower than those usually employed, being about 1 for the bog water and about 0.4 for the fen.

Using the usual laboratory procedures, a series of eight cultures of ten plants each was prepared and set up in the following conditions. (The bottles were embedded in peat surrounded by natural *Eriophorum* on Austwick Moss.)

1. Bog water unchanged.
2. Bog water—*pH* raised to 5.8 with NaOH.
3. Bog water—25 p.p. mill. of calcium added (as calcium chloride).
4. Bog water—25 p.p. mill. of calcium added; *pH* raised to 5.8.
5. Fen water unchanged.
6. Fen water—20 p.p. mill. of potassium added (as potassium chloride).
7. Fen water—*pH* reduced to 4.6 with HCl.
8. Fen water—20 p.p. mill. of potassium added; *pH* reduced to 4.6.

The nature of these alterations is obvious, alterations of *pH* value and calcium content first separately and then together, so that No. 4 solution is the bog water *changed into fen water* as far as calcium content and *pH* value are concerned. There is no feasible way of reducing the calcium content of the fen water, but its *pH* value and its basic ratio can be altered to resemble those of the bog, this being done first separately and then together. Unfortunately, the plants in solutions 7 and 8 were nibbled by hares and the cuttings had to be replaced. The results are, therefore, not comparable with those of the cultures 1 to 6. The plants were left for twelve weeks, the cultures being changed every three weeks. At the end of the first three weeks, the cuttings (like the surrounding vegetation) were only just beginning to grow owing to the uniformly low temperatures (peat and solutions at 6° C. at mid-day). The weather changed immediately afterwards and it was very bright and hot for all the subsequent period. In spite of this, the soil and solution temperatures *never exceeded* 14° C. and were usually 11–13° C.

The yields obtained, as percentages of the initial fresh weight, were:

Table XIV.

Solution	Total dry weight	Roots—dry weight	Series N.		Remarks on roots
			Fresh weight	Dry weight	
1	42.3	4.1	3.22		Good
2	43.5	4.45	3.49		Hairs and branches very marked (cf. 1)
3	41.5	4.4	3.30		Hairs and branches marked
4	37.7	3.55	3.36		Few hairs or branches
5	35.8	4.0	3.68		Long; few hairs or branches
6	40.8	5.3	3.41		Like 2 and 3
7	(33.1)	(2.7)	3.75		Like 4
8	(38.5)	(3.5)	3.62		Like 4; more branched than 7

It appears from these figures that *Eriophorum* grows less successfully in the fen water than in the bog water, although the differences are not large.

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The striking feature of the figures for yield is that altering the *pH* value and calcium content of the bog water to that of the fen water turns it, as far as *Eriophorum* growth is concerned, into a medium very similar to the fen water itself (cf. 4 and 5). The slight harmful effects of the fen water are overcome by the addition of potassium. The most noticeable feature of the appearance of the cultures was the striking difference in root appearance. The roots fall into three main types:

- (a) With approximately normal branch and hair development (1, 3 and 6).
- (b) With marked root hair development and very long branches (2).
- (c) With very short branches and few or limited hairs (4 and 5).

When it is remembered that in our laboratory cultures (containing similar proportions of calcium) low branching and small root hair development was associated with high calcium and low basic ratios, these results assume particular significance and they indicate that similar effects may be produced in natural soil solutions by the same factors. Since the calcium content of the bog water is slightly below the optimum, increasing the calcium absorption by raising the *pH* value should slightly improve the yield, as it did. Raising the calcium concentration to 35 p.p. mill. makes it just above the optimum and produces little alteration. The evidence, therefore, suggests that fen water is a less favourable medium for the growth of *Eriophorum* because of its less acid reaction, higher calcium content and lower basic ratio.

No description of the natural habitat factors would be complete unless it included some attempt to outline the water relations under which the plants normally grow. The fresh weight/dry weight ratios given in the above table show that the water content of the plants is very low. The variations in this ratio are probably not significant except that they suggest rather higher values in the fen water, the reverse of what one would expect from the higher calcium content and low basic ratio. We can, however, directly compare the natural conditions with those of the laboratory, since control cultures were carried out over the same period in the laboratory (L) and on the moss (M). These cultures were in solutions of type D, *pH* 6, calcium content 12 or 48 p.p. mill. and basic ratios 1.5 and 0.5. (Similar cultures (series H) were carried on in the laboratory at *pH* 4.5 and *pH* 7.0). Nothing in these cultures requires consideration except their water relations.

Table XV.

Series	No. of plants	Average	Solution temp.
		$\frac{\text{Fresh weight}}{\text{Dry weight}}$	
H (greenhouse; <i>pH</i> 4.5 and 7)	80	4.34	16–20° C.
L (artificial solutions in greenhouse)	40	4.38	16–20
M (artificial solutions on moss)	40	4.12	10–14
N (natural solutions on moss)	80	3.48	10–14

In the light of our previous discussion, it seems reasonable to attribute the smaller water content of the series M, as compared with series H and L, to the lower solution temperatures on the moss, although perhaps there may have been greater evaporation on the moss. This was not, however, clearly indicated by readings of wet and dry bulb thermometers and hence is not regarded as important. No such explanation will serve to explain the low water content of series N, which was growing within a few yards of series M and under precisely similar conditions. It is therefore probable that the peaty solutions used in series N exert some profound effect on the water relations of the plants. This supposition is borne out by the following facts. In early work on the reliability of methods, the fresh weight and dry weight of freshly gathered material, after preparation as cuttings, had been determined for plants from the usual source of our material, a moor above Guiseley, and also from a high level moss near Coniston. The fresh weight/dry weight ratios of these materials were respectively 3.52 ± 0.062 and 3.59 ± 0.071 . The water content of the natural material was thus as low as that of the *driest laboratory cultures*. Further, another series of cultures, in natural solutions, was carried out on Austwick Moss in a very sheltered position, to see how high the water content could be raised. The maximum value obtained for the fresh weight/dry weight ratio was 4.07, which is still low compared with most laboratory cultures, and much lower than the mean value of 4.80 for plants grown in culture solutions at the same time and place. Thatcher (30) has shown that peaty extracts increase the rate of transpiration in several species, and this observation offers a satisfactory explanation of the low water content of our natural cultures. It is possible that the toxic effect of peaty extracts, as demonstrated by Dachnowski (7), arises partly from the higher transpiration and consequent water shortage, caused by these extracts. The effects are due to some substance in solution and not to the hydrogen-ion concentration. While, as a whole, our cultures at pH 4.5 tend to show slightly lower water contents than those at pH 6 or 7, this effect is not significant in relation to the size of the probable errors, and it is negligible compared with that produced by the peaty extracts. Further, altering the pH value of peaty extracts does not necessarily alter the water content of the cuttings (cf. series N).

Since the water content of the plants grown in natural solutions is as low as that of plants grown under our driest laboratory conditions, it seems justifiable to assume that the effects of calcium are correspondingly pronounced, for it was demonstrated in a previous section that these effects disappear as the physiological humidity of the environment increases. It is clear that this conclusion is of great importance, because otherwise plants growing in a very wet habitat would only show calcium effects to an insignificant extent, unless the calcium concentration of the soil solution was very high.

A comparison of the culture series H, L, M and N serves to emphasise the point that the calcium and basic ratio effects become more pronounced as

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water conditions become more severe. We do not wish to conduct the reader through all the details of the twenty-four cultures, since the crucial point will be clearer if reference is made only to the data summarised below. It suffices to say that the growth of the cuttings in these various cultures was very uniform (cf. p. 14).

Taking the figures for "high calcium" we have:

Series	Calcium p.p. mill.	Solution temp. ° C.	pH	Root production*		Fresh weight Dry weight of tops	
				High basic ratio	Low basic ratio	High basic ratio	Low basic ratio
H	50	17-20	6.0	5.5	5.7	4.26	4.33
M	50	10-14	6.0	5.3	4.6	3.77	3.75
N	36	10-14	5.8	5.3 (vi)	4.0 (v)	3.41	3.68

* As percentage of initial fresh weight.

A low basic ratio becomes proportionately more harmful as the water content of the cultures decreases, and in spite of the lower calcium content of the solution. A further comparison shows that "low calcium" only produces a beneficial effect on water relations when these are intermediate as in series M.

Series	Calcium p.p. mill.	Fresh weight Dry weight of tops		Average "high calcium"
		High basic ratio	Low basic ratio	
H	10	4.10	4.14	4.30
M	10	4.08	4.19	3.76
N	10	3.49 (ii)	---	3.54

The effect of calcium on the water relations tends to be obscured either in the wetter conditions of the greenhouse or the drier conditions induced by natural soil solutions.

On the whole, these comparisons justify the conclusion that the effects observed in our cultural experiments fall into line with those observed in natural solutions, and it is now proposed to consider observations on the possible importance of these factors in nature. If these edaphic factors control the distribution of *Eriophorum* on such an area as Austwick Moss, then it ought to be possible to show that *Molinia coerulea* (dominant in the area called *fen*) will grow better in the fen water than *Eriophorum* and is not affected to the same extent by the higher pH, lime content, etc. In addition, we have to consider the further evidence for the assumption that the higher effective calcium content of the fen water is the factor to which is due the less favourable growth of *Eriophorum angustifolium* in that medium. Three cultures of *Eriophorum* have been carried out: I (in series N), early summer (eight weeks); II, June to August, nine weeks; III, August to December. *Molinia coerulea* was grown in both bog and fen waters alongside series II for comparison. The data are as follows:

Table XVI. *Comparison of effects of bog and fen waters.*

Series	Total dry weight*		Root—dry weight*		Fresh weight of green tops Dry weight	
	Bog	Fen	Bog	Fen	Bog	Fen
I	42.3	35.8	4.1	4.0	3.22†	3.68
II	45.8	32.8	5.12	2.22	4.05	4.07
III	22.8	22.5	4.05	3.0	4.16	4.05
<i>Molinia</i>	32.5	40.1	20.2	27.5	3.11	3.30

* As percentage of initial fresh weight.

† Probably low.

It will be noticed from these figures that *Eriophorum* grows better in the bog water and *Molinia* in the fen water. Although both plants grow satisfactorily in either solution, the differences are, in our opinion, sufficient to account for the distribution of these plants on this moss, bearing in mind that the severity of these effects would be greatly enhanced in nature by competition, and by the exposure to the edaphic differences over a long term of years. One or two points in the above table require further attention. In the figures for *Eriophorum* total dry weight, there is no difference in culture III because the tops of these plants showed no growth at all, but simply dried up as is usual in the autumn. The roots, however, showed a significant difference. The small difference in root weight in spring (I) may indicate a seasonal difference. The striking difference in the roots lies, however, in their appearance, and this is constant in all cultures. The plants grown in bog water have longer and more branched roots with an abundance of hairs. Both branches and hairs are poorly developed in fen water. In culture II roots in bog water were 30–35 cm. in length, while in fen water they were only 9–12 cm. long. The root hairs in I and III were 2–3 mm. long in bog water, rare and hardly visible in fen water. The branches in bog water were 10 cm. or more in length. In fen water they were rarely much more than 1 cm. There seems to be little doubt that these differences can be attributed in part, at least, to the higher effective calcium content of the fen water. There are indications also that this produces a distinct drying effect on *Eriophorum*. In the later cultures, II and III, a large number of the leaves were partly or entirely dead. The dried portions were therefore removed and weighed separately. The fresh weight/dry weight ratios given, therefore, refer to the *green* leaves only in order to obtain results comparable to those previously given. We can, however, get a comparison of the drying effects by comparing the dry weights of dead leaves with those of the green leaves.

Similar estimates were not made in culture I because the drying was slight and only affected the tips of a few older leaves at most.

These figures indicate a much greater proportion of dry leaves on the plants grown in fen water, and it may be suggested, in view of the earlier evidence, that this is probably due to the higher effective calcium content.

Series	Ratio of ^{Dead leaves} Green leaves (dry weights)		Total increase in weight per week*	
	Bog	Fen	Bog	Fen
I	Slight	Slight	1.91	1.1
II	0.313	0.408	2.09	0.64
III	0.745	0.795	Loss	Loss

* As percentage of initial fresh weight.

In culture III the autumnal decline is probably the dominant factor, in II this is beginning, in I it is naturally absent. It is of interest to note that when the drying of the leaves begins (II) the difference between the growth in bog and fen waters becomes more marked. This is quite in accordance with the conclusion (p. 20) that the calcium effect becomes more marked as the physiological dryness of the environment and plant increases. Since the plants in culture III made very little growth, marked difference in weight cannot be expected.

THE COMPOSITION OF NATURAL SOLUTIONS IN WHICH HEATH AND MOOR PLANTS GROW

In view of the difficulty in obtaining evidence as to the composition of the soil solution, evidence as to the effect of the calcium content and basic ratio of the natural media in which heath plants or moor plants like *Eriophorum* can grow has been confined to the following examples (Table XVII). These are analyses of the soil waters obtained by collecting it either from water-logged depressions or from pits sunk for the purpose. In only one case, the Coniston gravel delta, was the water level more than 25 cm. below the surface. Examples 1 to 5 in this table are analyses recently quoted by Graebner (10) and examples 6 and 7 have already been considered. Number 8 gives figures for the ground water of a dry gravel delta on Coniston Lake, the vegetation being an open colonising community of *Deschampsia flexuosa*, *Agrostis vulgaris*, with *Betula pubescens* and some willows (*Salix cinerea* and *S. aurita*). No. 9 is for water below a patch of coarse sand in the delta at the head of Ennerdale Lake, in which *Eriophorum angustifolium* was abundant. No. 10, the Ulls-water sample, is from below a gravel delta bearing an ash-willow wood, and No. 11 (Bassenthwaite) from below sandy alluvium covered with rich alluvial pasture. None of these last four habitats showed any appreciable peaty matter, the waters were all saturated with oxygen, and all possessed a similar but slight acidity. It seems permissible to argue that the mineral matters present in these cases are the chief determinants of the character of the vegetation. It must, however, be pointed out that the more heathy and moory vegetation types occurred on soils deficient in nitrates and nitrites, since no reaction was given with the diphenylamine test in these cases.

In this table, examples 2, 4, 6, 8 and 9 represent heathy types of vegetation. These, it will be seen, have low calcium content, 6–19.3 p.p. mill. and high

basic ratios, 1.3-0.77. The less heathy or moory types of vegetation occur in media of higher calcium content, more than 27 p.p. mill., and lower basic ratios, 0.65 to 0.06. Most of these samples have also a higher *pH* value, which would make the *effective* calcium concentration much higher. We think it evident that our experimental results deal with calcium concentrations of a range in which the dividing lines between moorland and non-heathy types of vegetation occur in nature. These results seem, therefore, to be directly applicable to the natural conditions.

Table XVII. *Analyses of soil waters (parts per million).*

No.	Habitat	K	+	Na	Ca	Mg	K + Na	pH
							Ca	
1	Meadow-moor	1.4		8.2	150	5	0.06	—
2	Heath	1.4		6.5	9.6	1.2	0.82	—
3	Meadow-moor	2.2		7.4	26.7	3.5	0.32	—
4	<i>Eriophoretum</i>	2.5		12.3	19.3	4.1	0.77	—
5	<i>Arundinetum</i>	4.5		15.6	30.8	6.1	0.65	—
6	<i>Eriophoretum</i> *		11		10	—	1.10	4.5
7	<i>Molinietum</i>		14		34	—	0.41	5.8
8	<i>Deschampsia-Agrostis</i> *		8.5		11	—	0.77	6.2
9	<i>Eriophorum</i> *		8		6	—	1.33	6.7
10	<i>Fraxinus-Salix</i>		7		31	—	0.22	6.2
11	Alluvial pasture		14		27	—	0.52	6.6

* Nitrates and nitrites absent.

THE PROBLEM OF CALCIFUGE HABIT IN THE LIGHT OF THE EXPERIMENTAL RESULTS

It is now possible to consider briefly the general problem presented by "calcifuge" species, in terms of our experimental data. It is true that these refer chiefly to bog species like *Eriophorum* as contrasted with *Molinia*. On the other hand, plants of drier soils, like *Deschampsia flexuosa*, show somewhat similar behaviour, and *Nardus stricta* may also resemble *Eriophorum*. Coulon (6) has shown that this species develops in normal culture solutions rapidly at *pH* 4.65, but with difficulty at *pH* 6.12, possibly because it absorbs too much calcium at the higher *pH* value, for, in addition, this author finds that Pfeffer's solution at *pH* 4.5 contains too much calcium for normal growth. The culture media employed by Rayner (22) for *Calluna* contained 117 p.p. mill. of calcium and had a high proportion of potassium and sodium to calcium (1.70). Since the solutions were apparently not changed in these experiments, the calcium content would be effectively very much less than the actual concentration named, since the calcium would be rapidly used up from the small quantities of medium employed. To the low effective calcium concentration and the high basic ratio the success of these culture media may be in part attributed. The large amount of work on *Sphagnum* (cf. Skene, 28) also shows many points of agreement with conclusions for *Eriophorum*. It may thus be possible to regard

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the present work as having a wider application to the general problem of the calcifuge habit.

No attempt will be made to consider three very definite aspects of this general problem which have not arisen in our cultures. It is clear that in the case of *Calluna* (and probably other Ericaceae) the effect of calcareous soils upon the endophytic fungi of the root is of the greatest importance, as is shown in a long series of studies by Rayner (21, 22, 23). It is equally well known that highly calcareous media cause chlorosis in many species, and in all probability this physiological effect would suffice to restrict the species to less calcareous media. Lastly, both Christ (3) and Tansley (29) have emphasised the importance of competition as a factor in determining whether a given species is *calcifuge* or *calcicole*, for in the absence of competition a species may be able to grow quite well on either type of soil. A parallel case in our cultures is probably that of *Eriophorum* and *Molinia* in *fen* and *bog* waters, in which each species did well, although in nature *Eriophorum* was confined to the *bog* water and *Molinia* to the *fen*.

Reverting, therefore, to the particular case under consideration in this paper, we have to enquire whether the plants of normal or calcareous soils differ in their calcium requirements from the plants of the moorland type. The following data for the two species, *Eriophorum angustifolium* and *Hordeum distichum*, serve to indicate that the latter species has in water cultures a higher calcium requirement when the two species are grown side by side for twelve weeks in the same series of solution.

Basic ratio	1.5	0.5	1.5	0.5
Calcium p.p. mill.	12	12	48	48
Solutions D, pH 6.5	I	II	III	IV
<i>Eriophorum</i> cuttings	100	61	88	76
Barley seedlings	44	67	100	21

(Ten plants in each case. Dry weight yield as percentage of the maximum.)

Further, *Brachypodium sylvaticum* resembled barley in growing best in solution III of the above series, while *Sesleria coerulea*, a plant rigidly confined to calcareous soils in the north of England would *only* grow in solution III of this series and grew much better in solutions of still higher calcium concentration. At first sight, these factors would appear to lend support to the supposition that the calcium concentration of the soil solution is normally the chief factor determining the distribution of these species to their characteristic soil types. The case is, however, more complex than it appears to be on a superficial examination.

Solution D		I	II	III	IV
Fresh weight	} <i>Eriophorum</i>	4.16	4.40	4.42	3.96
Dry weight		8.3	6.76	6.70	4.72
Transpiration*	} <i>Eriophorum</i>	7.70	7.75	7.81	7.95
		12.3	12.4	15.1	15.2

* As c.c. per week per gm. of fresh weight.

As the transpiration data and fresh weight/dry weight ratios show, the water content of *Hordeum* is far more affected by the changed calcium concentrations than is the water content of *Eriophorum*. The drying effect of high calcium is, therefore, by no means confined to moorland plants (cf. also Reed (24) and Hansteen-Cranner (11)) and apparently it is not more pronounced in these plants than in those of more normal type.

So far as the data will permit a conclusion, the position appears to be that the water relations will be optimum at different points in the case of different plants. Above these points, as shown in such series of cultures as those in the above table, the characteristic stunting of the roots is observed in *Eriophorum* (2 spp.), *Deschampsia flexuosa*, *Hordeum distichum* and *Brachypodium sylvaticum*. These effects begin at lower effective calcium concentrations for *Eriophorum* and *Deschampsia* than they do for *Hordeum* and *Brachypodium*. It is clear, therefore, that in habitats of equal physical humidity, one of the important factors controlling optimum water conditions will be the effective calcium concentration of the rooting medium.

It appears also to be probable that peaty moorland soils represent a distinct series of habitats which cannot be directly compared with normal inorganic soils. The mineral content of the soil solution is extremely low, and the evidence suggests that the calcium effects may only become evident because of the low water content these soils induce in plants growing on them. We attach considerable importance to these generalisations because they seem to reconcile many of the difficulties which are evident in the older view of the calcicole and calcifuge habits. The particular soil type on which a species grows will, on the present view, be determined by the integration of a whole complex of factors, of which we can at least recognise two climatic factors—humidity and temperature—together with the physical dryness of the soil, its calcium content, basic ratio, pH value, temperature, and the character and quantity of its organic matter. The *determining* factor may, therefore, in any one case, be either *climatic*, or the *physical* character of the soil or its *chemical* character, and there is no fundamental disharmony between these groups of factors. Salisbury (26) has given an excellent summary of the way in which the distribution of beech (*Fagus sylvatica*) and of other species is affected by climate and soil characters. Without referring to this in detail, it may be said that the general sequence is that many species tend to be indifferent to calcium or to occur on siliceous soils in drier climates, while they may be rigidly calcicole in moister climates. Similarly, Wheldon and Wilson (33) point out that a far larger number of species occur on calcareous soils in the humid climate of West Lancashire than are found on corresponding soils in the drier climate of Yorkshire. On the basis of our results, calcium sensitive species should be able to withstand higher concentrations of calcium in the more humid climate. It is well known that there are in this country a number of plants which may at times be found either on calcareous soils, on peat, or on dry siliceous soils

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(e.g. *Teucrium scorodonia*, *Juniperus communis*). Our results indicate that the common physiological character of these habitats would probably be their dryness. The effect of temperature is perhaps less clearly indicated in the literature. Without first-hand acquaintance with the facts, we have gained the impression that the character of the soil plays a comparatively unimportant part in determining the distribution of vegetation in tropical regions, and, if correct, this would be in harmony with our observation that high temperature reduces the calcium effect. If, on the other hand, calcium effects are produced more easily at low temperatures in calcicole species as well as in *Eriophorum*, this would serve to explain the fact that calcicole species (e.g. *Asplenium viride*) sometimes occur on siliceous rocks at high altitudes where mean temperatures are low (Lees, 13).

Without enlarging further upon these similarities, which involve the assumption that the effects of calcium are similar in different species, we would point out that the problem of the calcifuge habit appears to resolve itself very largely, from the ecological point of view, into the question of how the external conditions affect the humidity of plants. From the physiological point of view, there arises also the question as to why the calcium effects (e.g. on root production) are more pronounced in some plants than in others. The evidence, although inconclusive, suggests that calcium affects chiefly the distribution and physical state of the fatty components of the tissues, as shown by the effects on transpiration and root structure. The greater sensitiveness of the heath plants to calcium might then be associated with the production of larger proportion of fatty material, which, as pointed out by Priestley and Hinchliffe (18, 19), their structural features indicate. This point of view is, of course, open to the objection that plants with similar structural features may grow on normal or calcareous soils. The physiological peculiarities of moorland plants are also indicated by their ability to grow on soils of high hydrogen-ion concentration and in media containing toxic peaty substances, either of which are toxic to the majority of plants. The general position, therefore, seems to be that the moorland plants possess an all-round ability to thrive under a variety of conditions which are separately unfavourable to the majority of normal plants. When these conditions, low calcium, high hydrogen-ion concentration and peaty toxins, are present together, and often also, it must be remembered, in conjunction with nitrogen and oxygen deficiency and with low soil temperatures, the net result may well be to exclude every other type of plant on one or more grounds. It must be obvious, from these considerations and from the data in the earlier pages of this communication, that the problem of the calcifuge habit in plants is a question of extreme complexity. This, at any rate, is the impression which these investigations have implanted most deeply in the authors' minds.

APPENDIX

COMPOSITION OF CULTURE SOLUTIONS

STOCK SOLUTIONS.

		Gm. per litre	One c.c. contains
1	Calcium nitrate, $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	12.0	2 mgm. Ca
2	Potassium dihydrogen phosphate, KH_2PO_4	14.0	4 „ K
3	Magnesium sulphate, $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	20.0	2 „ Mg
4	Calcium sulphate, $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$	8.8	2 „ Ca
5	Calcium chloride, CaCl_2	5.5	2 „ Ca
6	Potassium chloride, KCl	7.5	4 „ K
7	Ferric phosphate	Saturated	—

The culture solutions were made up by taking the following numbers of cubic centimetres of the stock solutions, making up to a litre with distilled water and adding three drops of the saturated ferric phosphate solution.

Solutions A.

	I	II
Calcium nitrate	10 c.c.	20 c.c.
Potassium dihydrogen phosphate	15	15
Magnesium sulphate	2	2
Potassium chloride	—	15

Solutions B.

	I	II	III
Calcium nitrate	5 c.c.	5 c.c.	5 c.c.
Potassium dihydrogen phosphate	5	5	5
Magnesium sulphate	1	1	1
Calcium sulphate	—	20	95

Solution C.

Calcium nitrate, 30 c.c.; potassium phosphate, 30 c.c.; magnesium sulphate, 4 c.c.

Solutions D.

	I	II	III	IV
Calcium nitrate	6	6	6	6
Potassium dihydrogen phosphate	1.5	1.5	1.5	1.5
Magnesium sulphate	5	5	5	5
Calcium chloride	—	—	18	18
Potassium chloride	3	—	16.5	4.5

Solutions E.

Calcium nitrate	10	10	20	20
Potassium dihydrogen phosphate	20	10	40	20
Magnesium sulphate	2	2	2	2

Solutions F.

Calcium nitrate, 7 c.c.; potassium phosphate, 8.5 c.c.; magnesium sulphate, 15 c.c.

Solutions G.

Calcium nitrate	10	10	20	20
Potassium dihydrogen phosphate	15	30	30	60
Magnesium sulphate	2	2	2	2

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FAUNISTIC ECOLOGY OF SOME CARDIGANSHIRE STREAMS

By KATHLEEN E. CARPENTER

(*With one Sketch-map in the Text.*)

SUMMARY OF CONTENTS

I. The fauna of running waters, though studied in detail by some continental workers, has received little attention in Britain: the present study represents an attempt to summarise the ecological relationships prevailing in an area of some 150 square miles in West Wales, and to bring the results into line with the continental work. The main characteristics of the streams in this area are their origin, for the most part, in upland bogs, their consistent rapidity of flow, and the scanty proportion of dissolved materials, especially of lime, in their waters.

II. An outline scheme for classification of the faunal types is proposed: this, owing to the wide range of variation in physical conditions, is based upon ecological type rather than upon determination of dominant species. The first grade in classification is taken as the "Biosynoecium" (*sensu* Enderlein); within each biosynoecium the "animal associations" are described as follows:

- A. The surface-film association.
- B. The free-swimming association of the middle waters.
- C. The limnophilous association.
- D. The phytophilous association.
- E. The lithophilous association.

III. The running waters of the Cardiganshire area are classified as follows:

A. Moorland waters of the high plateau:

- A 1. Eaux sauvages.
- A 2. Swamp-streams.
- A 3. Cascade-reaches.

B. Waters of the lower coastal area:

- B 1. Short streams, mainly spring-brooks confined to this section.
- B 2. Lower courses of longer rivers, rising in the plateau-bogs.
 - (a) Gorge-sections.
 - (b) Lower plain-sections.

The characteristic animal-associations are enumerated.

IV. Comparison of lists of species shows that there is little variation in type between highland and lowland reaches, beyond that which is directly

dependent upon topographical factors: the streams remain "torrential" in character almost to sea-level, and species established as stenothermous post-Glacial relicts occur in general throughout their courses. The distribution of Planarian species is peculiarly interesting in this connection. *Planaria albissima* Vejd., a species not elsewhere recorded from Britain, is widely distributed throughout the area.

I. THE FIELD OF INVESTIGATION

The study of the macroscopic fauna of Cardiganshire trout-streams was first undertaken as accompaniment and background to the writer's investigation of the problems of mineral pollution in this county: it has since been carried further, and some attempt has been made to classify the animal communities on an ecological scheme. The Cardiganshire area itself has been very little worked by collectors, but in any case there seems to be a singular dearth of British studies dealing with the fauna of running waters. Public attention has recently been called (see *Nature*, June to December, 1924) to the need for "fundamental studies" on this topic, but the writer has found no British work available for comparison. Shelford's work on *Animal Communities in Temperate America* includes a valuable chapter on "the animal communities of streams," but the only considerable body of literature on the subject is formed by the scattered papers of continental workers on the fauna of streams of the highlands of Central and Northern Europe, published mainly in the *International Review of Hydrobiology and Hydrography* (Leipzig), *Archiv für Hydrobiologie* (Stuttgart) and *Annales de Biologie Lacustre* (Bruxelles), and dealing principally with the fauna of mountain-brooks of "torrential" character. With these, the Cardiganshire streams in certain of their reaches may aptly be compared: although the elevation is not great (the highest point, in the east of the county, is 2468 ft. or 752 m.), the steep slope of the ground and the rocky substratum give to many of the streams a torrential character; but one salient feature of the majority of the streams is their origin from stretches of peat-bog in the uplands, and another the variety of ecological types to be met with at close quarters.

The area is flanked on the east by the Plynlimon plateau, while on the west cliffs of 200 ft. and upwards descend steeply to the sea. There is a great sameness of geological structure, the rocks being mainly Silurian grits and shales, save where anticlinal folding and faulting bring up older Ordovician strata in the eastern region: the rocks weather to a thin, light soil which is notoriously deficient in lime. There is a somewhat abrupt transition, corresponding pretty well with the outcrop of the older rocks, between the lower, or coastal plateau (elevation about 400 to 900 ft.) and the "high plateau" or Plynlimon region of the east: this latter is a plateau well dissected by the valleys of streams which draw their head waters from the peat-bogs and whose main courses are east to west down the slope facing the sea and fronting the

prevalent west and south-west winds. There is no coastal plain, properly speaking; any level land lies in ribbon-like strips along the valleys of the main rivers, and its extent, though still small, owes increase to the glacial action which has gouged out these valleys and thinly carpeted them with boulder-clay. The latter, though certainly the most productive soil of the neighbourhood, is derived from rocks of the neighbouring uplands, and this brings no considerable addition of true "clay" or lime.

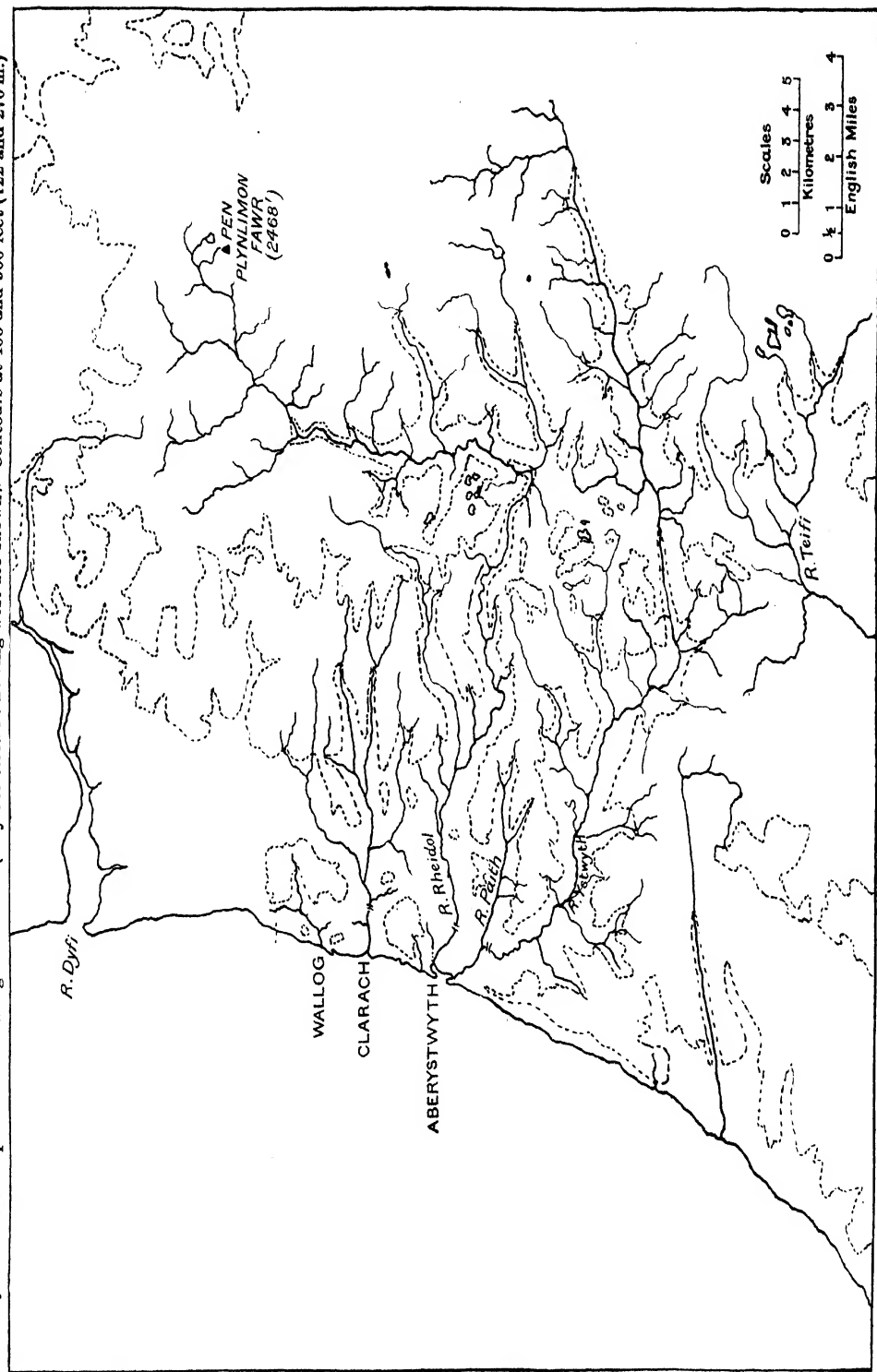
The climate, on the whole, is equable, though considerably colder on the plateau, where snow, a rare phenomenon nearer the coast, may lie for days together in winter. The abundant rainfall (46.49 ins. at Aberystwyth, 65.2 ins. at Devil's Bridge, on the edge of the high plateau) provides an ample supply of water: the streams are thus numerous and usually rapid in flow throughout their courses: some of them have developed rocky gorges in their middle sections, which either mark the base of a sudden change of level or coincide with lines of faulting in the rocks. The geologically recent subsidence of the coastal plain has had the effect of almost completely eliminating the usual phases of slackened flow and sedimentary deposition which mark the lowest section of a normal river-valley. Some deposition takes place here, it is true, but it is almost entirely that of rough grit, pebbles and boulders, which in flood times form fresh banks, between which the river runs its shifting course, and only here and there the old fluvio-glacial clays of the lower valleys contribute a certain amount of really finely divided material.

The rapid flow and frequency of cascades keep the waters thoroughly well oxygenated, and they are throughout remarkably free from dissolved solids. Analyses of water from the lower reaches of two of the streams showed the total solid content in grains per gallon to be 3.36 in the one case, 2.80 in the other, with sodium chloride 1.32 and 1.89 respectively: there is practically no organic matter in solution as a rule, though some of the plateau waters have a faint brown peat-coloration. The hardness is usually 1 (one), and the reaction slightly acid (*pH* 5.8 to 6.0 in the bog-streams to *pH* 6.8 in purely lowland brooks); the lime content is small. Two samples, one from a stony plateau brook of *pH* 6.2, the other from a lowland brook of *pH* 6.8 in February, were found to contain lime as follows:

CaO equivalent	2.52	mg.	per	litre	in	the	plateau	brook
"	"	11.62	"	"	"	"	lowland	brook

These figures, selected as the highest obtainable from brooks of their respective types, even so, are low as compared with those quoted from other districts. The total dissolved solids in the Sauerland brooks of Westphalia, as ascertained by Thienemann (1), varied up to 116.2 mg. per litre, and CaO up to 40.4 mg. per litre, while in Rügen (2) the same worker found total solids up to 484, CaO up to 145 mg. per litre, in solution.

Physical sketch-map of the mid-Caradiganshire area (only the streams flowing west are shown). Contours at 500 and 300 feet (152 and 210 m.)



II. ECOLOGICAL CLASSIFICATION

Thienemann, in his study of the brooks of the Sauerland (1), divides the course of a typical hillcountry stream into three biocoenotic regions:

- (a) the springs and spring-brooks,
- (b) the trout-beck, and
- (c) the region of dominance of Cyprinidae, where the current is less rapid and muddy and weed-grown reaches abound.

To this standard type the mid-Cardiganshire streams do not wholly conform: the majority of them originate from peat-bogs, and, once established as trout-streams, remain through practically the whole length of the course in this latter class, the peaceful Cyprinid-dominated reaches being conspicuously absent, though there is in the lower courses a certain alternation of rapid and quieter sections. These peculiarities, while dictating an immediate classification into (a) moorland waters of the high plateau, and (b) waters of the coastal region, at the same time involve a degree of variation in ecological type at short range which renders further classification a matter of some difficulty, especially as no universal system of nomenclature for use in freshwater ecological studies has yet been evolved. Shelford, in his study of "animal communities" (3), introduces a whole series of grades of classification—mores, consociés, stratum, association, formation, . . . , but in his outline sketch of stream communities uses all but one of these terms at the same level of classification—an instance of the difficulties of exact delimitation in such work. Thienemann and other continental workers, treating of the larger habitat groups as "biotopes" or "biosynoecia" ((4) and (5), (6) and (7)), proceed directly to the consideration of lists of species, grouped according to the typical situation in which each occurs. For the purposes of the present study, it seems well, while avoiding a rigid scheme of classification to which it is impossible strictly to adhere, to regularise the terminology in some slight degree in the combined interests of brevity and clearness. The use of the obvious term "community," as indicating a group of animals found together in a characteristic situation, will be avoided, this term being inevitably associated with its classical use by Petersen in descriptions based upon quantitative investigation of the fauna of the sea-bottom. Petersen himself remarks (8) that "strange as it may seem, there does not exist any survey of the animal communities upon land based upon quantitative investigations of the commoner species": the fact is equally true as regards running waters, and here at least it is not so strange as it may appear, since the conditions in streams may vary so greatly within a short radius that faunistic study must perforce take as its unit the area characterised by a particular set of topographical factors, and will thus be based upon ecological type rather than upon the determination of dominant species. The first grade in classification will thus be taken as the "*biosynoecium*" (*sensu* Enderlein (5)), within which will be

recognised various "associations," each made up of the animals found in a certain characteristic situation, e.g. at the water surface, on the bottom-mud, on stones, etc. Within each type of "association" there may exist several types of habit, an outline of which follows here.

A. THE SURFACE FILM ASSOCIATION.

This comprises two main types: (1) the "surface-skimmers," of predaceous habit, with light bodies and spreading limbs, which dart actively about the surface-film in pursuit of food, exemplified by *Velia currens* and *Gerris lacustris* (Water-crickets, Water Measurers), and (2) very small, light-bodied forms which hang downward from the surface-film and are usually microphagous in habit, e.g. some Dipteran larvae, as *Stratiomys*.

Both these groups are important only in calm waters, since the streaming of a definite current naturally does not encourage the development of either plankton or surface-film associations. In backwaters and calm eddies the surface-skimming Hemiptera may, however, be quite numerous.

B. THE FREE-SWIMMING ASSOCIATION OF THE MIDDLE WATERS.

This includes carnivorous types such as Fishes, Dytiscid Beetles and some Hemiptera (especially Corixidae): most of them are limited to backwaters and calm reaches, but some stream-fishes, especially trout, are found in the current itself, in virtue of their muscular force and positive rheotaxy.

C. THE LIMNOPHILOUS ASSOCIATION.

Members of this group (constituting the true "bottom fauna") lie buried in the bottom deposit or crawl upon its surface: they are best represented in quiet reaches of rivers, where fine mud can accumulate, and they exhibit considerable divergence of type. (1) The mud-burrowing habit is characteristic of sluggish microphages, such as the little bivalve *Pisidium*, the Oligochaete *Tubifex*, a few Ephemeroidea (*Siphonurus*), *Sialis* larvae, and Dipteran larvae of the *Chironomus* and *Tanytarsus* types, but a few highly predaceous species, such as the larva of *Cordulegaster* (Odonata), also adopt it by way of ambush. (2) More usually, predaceous limnophiles crawl upon the mud-surface, as leeches and some Hydrarachnida, larvae of *Dytiscus* and many Agrionidae, and some vegetarians, such as *Limnaea truncatula* and *L. pereger*, may also adopt this habit. Some Ostracoda are limnophiles, but very few of them occur in running water. (3) A few types, Tabanid larvae in particular, are characteristically found in sand or gravel, but, as a rule, such situations are almost barren.

D. THE PHYTOPHILOUS ASSOCIATION.

Three classes of plants are important in running water: the Bryophyta, commonly found encrusting stones in rapid streams, the Algae, most charac-

teristic of backwaters, and the aquatic Phanerogams, which are only abundant in calm waters where there is mud for their rooting.

(1) The fauna of the Phanerogam tufts consists mainly of vegetarian types, and especially larvae of the Limnophilidae, which depend upon the plant-growth for food, support and often for material for the construction of their protective cases. Some small Crustacea, especially *Canthocamptus*, are particularly associated with Phanerogamic plant-growth, and even such a carnivorous type as *Polycelis nigra* must rank as a phytophile, since by day, at any rate, it is usually to be found crawling over water-weeds. On the other hand, the vegetarian, *Limnaea pereger*, ranks in this scheme as a limnophile, being most usually found on the bottom mud, although it may climb up the water-plants to deposit its eggs (in many small brooks the egg-masses are found on the mud or even on stones); and *Ancylus fluviatilis*, also a vegetarian, is a lithophile, resting on the surface of stones.

Certain small beetles, while free-swimming in habit, are so constantly found round about the tufts of Phanerogams as perhaps to deserve mention here: species of *Hydroporus*, *Platambus* and *Helophorus* frequently occur in this way.

(2) The slimy filamentous Algae (*Spirogyra*, *Zygnema*, etc.) of the backwaters do not afford convenient shelter for a rich fauna—a few types, however, are particularly associated with them in occurrence. Among these, small Hydrophilid beetles (especially *Hydraena*) are frequent, and most characteristic are a few Trichopteran larvae of the Polycentropidae, such as *Plectrocnemia conspersa*, which shelter in a tangle of silken threads among the filaments.

(3) The Bryophyta of the rapid reaches are highly important as giving shelter to a rich fauna of very varied types. Most conspicuous are perhaps the Crustacea *Gammarus pulex* and *Asellus aquaticus*, the former usually found among submerged mosses (*Fontinalis*), the latter among encrusting liverworts such as *Fegatella*; Parnid beetles (*Elmis*, etc.) are particularly abundant in the Bryophyte growth, and other Coleoptera such as *Hydraena*, *Anacaena*, *Agabus*, commonly shelter here; this is the best hunting ground for water-mites, several Dipteran larvae (of *Orthocladus*, *Pericoma*, especially) frequent it, and it is a general resting-place for young larvae of several other insect-groups (Ephemeridae, Perlidae and Trichoptera) which in their later stages rank as "lithophiles." Stone-fly larvae of the genera *Nemura*, *Leuctra* and *Nephelopteryx* prefer the shelter of the Bryophytes throughout their aquatic life. Steinmann (9) has called attention to the frequent occurrence of strongly-curved or hook-like spinous processes on the limbs of the typical Bryophyte-dwellers, which serve to anchor them against the streaming of the rapid current sweeping past the stones.

E. THE LITHOPHILOUS ASSOCIATION.

These animals, associated with the neighbourhood of rock or stone, occur in greatest numbers in the swift reaches of a young stream, where they form

the dominant group, and many of the lithophilous species are numbered in Steinmann's list of "echte Bachtierre" (9), peculiar to rapidly flowing waters, stenothermous at low temperatures, and probably relicts of the Glacial Period, surviving in scattered highland brooks, as distinguished from the more cosmopolitan "eurythermous" types (including many limnophiles, phytophiles, etc.) which have a wide distribution in slow and rapid streams and even sometimes in standing waters. Certain types of lithophile, however, may be found even in quiet lowland reaches where small stony patches occur. Three main types of lithophilous habit may be distinguished, as follows:

(1) *The stone-clingers*, among which larvae of most Plecoptera and many Ephemeridae are numbered, are typical current-dwellers, and show many beautiful adaptations to this habit (10). A particularly good example found in Cardiganshire streams is the larva of the Ephemerid *Ecdyurus lateralis*, which is common in cascades and rapids. The body is strongly flattened dorsiventrally, and roughly wedge-shaped, tapering from the broadly-elliptical, depressed head to the last abdominal segments, whose three caudal filaments are long and slender and spread closely along the stone to which the whole body is pressed. The animal clings firmly by its three pairs of thoracic legs, themselves markedly flattened in the general plane, and spread radially like the hooks of a grapnel—so firmly that even when the stone is lifted from the water, the animal is with difficulty dislodged, and in the natural situation it seems able to endure the force of the swiftest current. This type of dorsiventral flattening, associated with the stone-clinging habit, and coupled with the reduction of fringing hairs or leaf-like projecting gills, is seen, though in some cases less perfectly developed, in several other Ephemerids and some Plecopteran larvae commonly found in rapid streams.

A stone-clinger of quite another type, though equally successful in a similar environment, is *Ancylus fluviatilis*, the freshwater limpet, which is particularly common on the upper surfaces of stones in small cascades and rapids. The conical shell is kept closely drawn down to the level of the stone, to which the animal firmly adheres by its flattened sole-like foot, the intimate contact of the two moist surfaces effectively resisting forces of dislodgment. A similar sucker-like mode of adhesion is adopted by the microphagous larvae of the Dipteran *Simulium* (*Melusina*), which, adhering to stones by the flattened posterior portion of the body, allow the head region to stream out on the swift current without risk of being swept away: these larvae, in moving from place to place, guide and steady themselves by hooking the "prothoracic claws" over the threads of a labyrinth which they spin over stones and weeds (11). Some leeches (*Glossiphonia* and *Haemopsis*), though often found on the mud-surface, may rank also as stone-clingers, adhering by their suckers, and depositing their eggs in capsules glued to the stones. As stone-clingers also, though of still another type, might be classed the larvae of Rhyacophilidae, which, freely moving in the larval phase, build roomy pupa-cases of small

pebbles, and glue them firmly down to the stone-surface in regions of swift current; but such species must, perhaps, rather be placed with regard to their usual mode of life, in the second group of lithophiles.

(2) *Stone-shelterers*. Many Trichopteran larvae (e.g. *Agapetus*, *Mesophylax*, *Apatania*) use small pebbles to build portable larval-cases which are large and heavy relatively to the size of the larva, and which doubtless serve as "ballast" to prevent sweeping away by the current, a danger which is also minimised by the habit of creeping into chinks between larger stones. Some few (e.g. *Silo*, *Goera*) add further ballast by lateral attachments of larger flattened pebbles. The pupa-cases of such types are usually fixed to stones.

Hydropsyche, sheltering in a crevice, weaves a snare of silken secretion which, spread in the path of the current, catches small food-particles and relieves the builder of the necessity to wander in exposed places.

(3) *Hygropetrical types*, the third class of lithophiles, are usually small-bodied forms which crawl in the water-film against the lower surfaces of stones. Perhaps the most interesting of these are the Turbellaria Tricladida, of which several species are confined to running waters, and two (*Planaria alpina* and *Polycelis cornuta*) are considered as classic examples of the post-glacial relict population of highland brooks. All are carnivorous, and markedly light-shy, sheltering under stones by day, and at night preying upon Insect-larvae, worms, etc. The most numerous of hygropetrical forms are larvae of certain species of Diptera (e.g. *Dixa* spp.), worm-like in shape and small in bulk, which wriggle against the stone-surface by pushing head and tail against it alternately, and feed by ciliary currents. Many of these types are found in calm reaches as well as in the swift current.

III. FAUNISTIC ECOLOGY

NOTE ON IDENTIFICATION OF SPECIES.

Since so large a proportion of the fauna of running waters is composed of the larvae of Insects, accurate identification of species is a matter of considerable difficulty. Many of the larvae of Diptera, especially, have not been described even by genera, far less by species; in such cases the method adopted wherever possible was to breed out and identify the adults. Where this was not possible, the larvae were classed as nearly as could be achieved, sometimes into genera, occasionally only into some generic group. For their assistance in the work of identification, my grateful acknowledgments are due to the following: Mr J. R. le B. Tomlin and Mr F. Balfour-Browne (Coleoptera), Mr F. W. Edwards and Mr T. E. Collin (Diptera), Mr K. G. Blair (Ephemera and Plecoptera), Mr C. G. Robson (Mollusca), Mr C. D. Soar (Hydracarina), and Mr H. Whitehead (Turbellaria Tricladida).

A. MOORLAND WATERS OF THE HIGH PLATEAU.

In the upper part of the plateau and between the shoulders of the hills are extensive peat-bogs where pools of acid moorland water (usually pH 5·8–6·0) lie in the hollows, and small wandering streams take origin, later to collect on the steeper slopes into true moorland brooks. These “eaux sauvages,” fringed by *Lycopodium*, heaths and *Carex*, and floored by peaty deposits and *Sphagnum*, lead almost insensibly on to the upper courses of the brooks, the chief distinction being that of gradient and consequent rate of flow; still the distinction is sufficient to necessitate a separate consideration of the two. As a rule, the streams leading directly from the peat-bog-divides flow rapidly along narrow channels which, though flanked by marshy ground overgrown with sedges, are yet clearly marked off by the swiftness of the stream, which bears with it vegetable-débris from the bogs. A later section of the same stream, reaching the steep slope near the plateau’s edge, will fall into a series of cascades over the rocks which are there exposed. There are thus three definite types of running water in the high plateau—the eaux sauvages, the swamp-stream, and the cascade-reach—each with its appropriate fauna.

A 1. Biosynoecium of the eaux sauvages.

The true aquatic fauna is very scanty here: lithophilous types are absent for lack of stone-surface, the plant-growth is not of a type to afford shelter to a rich variety of phytophiles, nor is the peaty débris of the bottom an attractive resting-place: such few types as do occur are mainly limnophiles or surface-skimmers, but a very interesting “free-swimmer” is the web-footed Newt (*Triton palmatus*), which seems confined to the high levels in this district.

The characteristic species are as follows:

Limnophilous and hygropetrical associations.

Stylaria lacustris (Oligochaeta)

Orphnephila testacea (Diptera—larval)

Cypris virens (Ostracoda)

Chironomus sp. (Diptera—larval)

Siphonurus arnatus (Ephemera—larval)

Surface-film association.

Gerris gibbifera (Hemiptera)

Gyrinus natator (Coleoptera)

Isotomurus palustris (Collembola)

Culicidae spp. (Diptera—larval and pupal)

Free-swimmers.

Hydroporus pubescens (Coleoptera)

Triton palmatus (Amphibia)

A 2. Biosynoecium of the swamp-streams.

This is very similar in basic type to A 1, but much richer in species, by the addition of many types which thrive in a more rapid current: *Triton palmatus* is not found here.

Characteristic Limnophiles are:

Tubifex tubifex (Oligochaeta)
Stylaria lacustris (Oligochaeta)
Ei-rudo medicinalis (Hirudinea)
Haemopsis sanguisuga (Hirudinea)
Herpobdella octoculata (Hirudinea)
Siphonurus lacustris (Ephemera—larval)
S. armatus (Ephemera—larval)

Nemura standfussi (Plecoptera—larval)
Ischnura elegans (Odonata—larval)
Chironomus sp.; plumosus group (Diptera—larval)
Tanytus nebulosus (Diptera—larval)
Limnaea pereger (Mollusca—rare)

Phytophiles, found on and about the projecting strands of sedges which swing out with the current, are:

Podura aquatica (Collembola)
Polycelis nigra (Tricladida)
Planaria albissima (Tricladida)
Simulium reptans (Diptera—larval)
Anabolia nervosa (Trichoptera—larval)

**Limnophilus bipunctatus* (Trichoptera—larval)

**Mesophylax impunctatus* (Trichoptera—larval)
Eurycercus lamellatus (Cladocera)
Cyclops serrulatus (Copepoda)
C. fuscus (Copepoda)
Anacaena globulus (Coleoptera)

[** The species indicated, though vegetarians, require small pebbles for the construction of larval and pupal cases, and hence are only found where at least a few such occur—not in the very highest reaches of the bog-streams.]

Free-swimmers, which in this case rank almost as phytophiles, are a few Coleoptera only, and these usually of small size: quite frequent are:

Hydroporus obscurus
H. pubescens
H. rivalis

Agabus paludosus
A. chalconotus

Larvae and pupae of Culicidae also occur.

Surface-skaters are:

Gerris gibbifera (Hemiptera)
Velia currena (Hemiptera)

Isotomurus palustris (Collembola)

A 3. *Biosynocium* of the cascade reaches.

Where the stream splashes from step to step of a rocky bed, strewn with detached boulders, there can be little accumulation of mud, and the successful types are mainly stone-clingers and hygropetrical forms; to the sides of the main current or at the foot of a cascade are often quieter waters where a few free-swimmers may be found, and a scanty growth of encrusting Liverworts or filamentous Algae may shelter a variety of animal-species.

The **Lithophilous association** is distinctly dominant, and characteristic species are as follows:

Ecdyurus lateralis (Ephemera)
Baëtis vernus (Ephemera)
Isogenus sp. (Plecoptera)
Nephelopteryx sp. (Plecoptera)
Leuctra incernis (Plecoptera)
Dixa maculata (Diptera)
Simulium latipes (Diptera)

Rhyacophila obliterata (Trichoptera)
Agapetus fuscipes (Trichoptera)
Silo nigricornis (Trichoptera)
Apatania fimbriata (Trichoptera)
Hydropsyche angustipennis (Trichoptera)
Ancylus fluviatilis (Mollusca)—(rare)

while *Planaria albissima* (Tricladida) and *Orphnephila testacea* (Diptera—1) are characteristically “hygropetrical” types.

Planaria alpina is also found in some of these streams.

Phytophiles and free-swimming semi-phytophiles are:**(a) Associated with Algal growth:**

Plectrocnemia conspersa (Trichoptera)
Cyrnus insolutus (Trichoptera)

Halesus digitatus (Trichoptera)
Agabus bipustulatus (Coleoptera)

(b) Associated with Bryophytes, or free in the water:

Tanypus nebulosus (Diptera)
Limnophilus decipiens (Trichoptera)
Hydroporus Davisii (Coleoptera)
Limnebius truncatellus (Coleoptera)

Elmis aeneus (Coleoptera)
Corixa limitata (Hemiptera)—(rare)
Asellus aquaticus (Isopoda)

Of true free-swimmers, only two species of fishes occur: the brown trout (*Salmo fario* var. *cambrensis*) is very common in these upland streams, and the minnow (*Leuciscus phoxinus*) occurs in a few of them.

B. STREAMS OF THE COASTAL REGION.

These may be conveniently divided into:

1. *Shorter streams*, rising below the edge of the high plateau.
2. *Lower courses of longer rivers*, which rise in the plateau-bogs.

The distinction is more than one of mere length: in the first place, the waters of the short streams are rather less acid than those of the longer rivers (pH round about 6·8 instead of 6·4), and, in the second, the former are far less subject to sudden flooding than those deriving from the true uplands, so that their valleys are not covered by gravel flood-deposits but expose the strata of the solid rock, or, in many places, its carpet of glacial and fluvio-glacial deposits.

B 1. *The short streams.*

The "spring brooks" are, on the whole, rather of the rheocrene type, i.e. rapid streams with stony courses, loose boulders, and vegetation predominantly Bryophytic, but some, at any rate, verge upon the limnocrene, where they flow in deep glaciated valleys with well-marked clayey deposits: this latter type is particularly noticeable in the brooks of the Clarach system, which runs through a fine glaciated valley westward to the sea. In such cases the lithophilous association, usually dominant, gives place to a group of limnophilous types and of phytophiles which are associated with the presence of such rooted Phanerogams as *Callitriche verna*, *Ranunculus aquatilis* and *Veronica beccabunga*.

These weedy masses shelter a large phytophilous association which in some respects strongly resembles that of the low ponds, but differs from the latter in the abundance of Caddis larvae. These always cluster particularly around the *Callitriche* clumps, which seem to afford better shelter than the *Ranunculus* with its much-divided submerged leaves—better housing-material, too, for forms like *Limnophilus decipiens*, which here builds its case entirely of the delicate leaves of the Starwort, as does *Anabolia nervosa* in the young stage, while others rely on drifting leaves, bark and twigs from the over-hanging

trees. The complete list of Trichoptera found in these weedy situations is as follows:

Crunoecia irrorata (case horn-like, of vegetable matter)
Brachycentrus subnubilus (case quadrangular, of vegetable matter)
Plectrocnemia conspersa (no larval case; silken threads among Algae)
Anabolia nervosa (case cylindrical, of leaves, etc., with trailing twigs)
Limnophilus decipiens (case entirely of leaves)
L. flavicornis (case of small bits of stalk, etc., set crosswise)

Polycelis nigra crawls over the weeds and *Planorbis glaber* may often be found upon them: *Simulium reptans* fixes its pupa-case to their trails, and Trout and Sticklebacks shelter beneath their mass. In the mud accumulated at their roots lie small Lamellibranchs (*Sphaerium corneum*, *Pisidium nitidum*), and Oligochaetes and *Chironomus* build their tubes—*Limnaea pereger* and *L. truncatula* crawl upon its surface, and Dragon-fly larvae abound in it: of Odonata, *Ischnura elegans*, *Platynemis pennipes*, *Agrion pulchellum* and *Cordulegaster annulatus* are especially numerous here. Among Leeches, both *Haemopsis sanguisuga* and *Hirudo medicinalis* occur, but the commonest species is *Glossiphonia complanata*, a Clepsinid type with a taste for *Limnaea pereger*.

One Ephemerid larva (*Siphonurus lacustris*) frequents the mud, and one Plecopteran (*Nemura standfussi*) is found on mud-coated stones, often together with the Dipteran *Dixa nebulosa*. The Alder-fly (*Sialis flavilatera*) larva is found in reaches overhung by trees; Hemiptera are well represented: water-skimmers are *Gerris lacustris*, *Velia currens* and *Hydrometra stagnorum*; *Corixa limitata* and *Sigara minutissima* swim in the clear waters near the banks, and *Podura aquatica* (Collembola) is abundant at the surface. Several species of Copepoda, Cladocera and Ostracoda have been identified—special mention must be made of *Canthocamptus minutus* and *Ca. staphylinus* (both found on weeds), which have never been found locally in any other situation, save in the "impermanent trickles" of the roadsides. Crustacea-Malacostraca are represented by *Asellus aquaticus*, which occurs pretty generally here, and *Gammarus pulex*, which is much more limited in distribution, being confined entirely to a few brooks of the class now under review. Coleoptera are numerous, Dytiscidae, etc., swimming freely, Parnidae living on moss-grown logs and stones, *Anacaena* and *Limnius* often tangled in Algal filaments.

Where rock-outcrops or loose boulders appear in the beds of these "short streams," the whole regiment of "stone-clingers" take the field, most noticeable being the flat-headed Ephemerid and Plecopteran larvae (*Ecdyurus lateralis* and *Baëtis tenax*, *Dictyopteryx mortoni*, *Isopteryx torrentium* and *Leuctra inermis*), and those caddis-worms which build pebble-cases, or silken nets under stones. Trichoptera of these stony regions are: *Rhyacophila oblitterata*, *Agapetus fuscipes*, *Glossosoma vernale*, *Silo nigricornis*, *Philopotamus montanus*, *Hydropsyche angustipennis*, *Diplectrona felix*, *Limnophilus bipunctatus* and *Mesophylax impunctatus*.

On stones above the water-surface but splashed by its spray, the Brook-limpet, *Ancylus fluviatilis*, is abundant, and *Limnaea pereger* comes here some-

times in search of Algae and Diatoms. On the under-surface of stones near the water's edge, Dipteran larvae of the *Dixa* type are common, also the Triclad *Planaria albissima* and, in certain special localities, *Planaria alpina* and *Polycelis cornuta*. The dominant types of the lowland brooks in their different facies may be enumerated as follows:

Surface-skimmers.

<i>Hydrometra stagnorum</i> (Hemiptera)	<i>Velia currens</i> (Hemiptera)
<i>Gerris najas</i> (Hemiptera)	<i>Gyrinus natator</i> (Coleoptera)

Free-swimmers and Semi-phytophilous swimmers.

<i>Salmo fario</i> (Pisces)	<i>Hydroporus rivalis</i> (Coleoptera)
<i>Gastrosteus aculeatus</i> (Pisces)	<i>Deronectes latus</i> (Coleoptera)
<i>Agabus bipustulatus</i> (Coleoptera)	<i>D. depressus</i> (Coleoptera)
<i>A. chalconotus</i> (Coleoptera)	<i>Corixa limitata</i> (Hemiptera)
<i>Platambus maculatus</i> (Coleoptera)	<i>Sigara minutissima</i> (Hemiptera)

Lithophiles.

<i>Planaria albissima</i> (Tricladida)	<i>Leuctra inermis</i> (Plecoptera)
<i>Pl. alpina</i> (Tricladida)	<i>Isopteryx torrentium</i> (Plecoptera)
<i>Polycelis cornuta</i> (Tricladida)	<i>Rhyacophila oblitterata</i> (Trichoptera)
<i>Ancylus fluviatilis</i> (Mollusca)	<i>Agapetus fuscipes</i> (Trichoptera)
<i>Ecdyurus lateralis</i> (Ephemera)	<i>Hydropsyche angustipennis</i> (Trichoptera)
<i>Baëtis tenax</i> (Ephemera)	<i>Mesophylax impunctatus</i> (Trichoptera)
<i>Dictyopteryx mortoni</i> (Plecoptera)	<i>Dixa maculata</i> (Diptera)

Limnophiles.

<i>Dendrocoelum lacteum</i> (Tricladida)	<i>Ischnura elegans</i> (Odonata)
<i>Pisidium nitidum</i> (Mollusca)	<i>Platycnemis pennipes</i> (Odonata)
<i>Limnaea pereger</i> (Mollusca)	<i>Siphonurus lacustris</i> (Ephemera)
<i>L. truncatula</i> (Mollusca)	<i>Chironomus</i> sp.; plumosus group (Diptera)
<i>Tubifex tubifex</i> (Oligochaeta)	<i>Tanytus nebulosus</i> (Diptera)
<i>Nais elinguis</i> (Oligochaeta)	<i>Orthocladus stercorarius</i> (Diptera)
<i>Herpobdella octoculata</i> (Hirudinea)	<i>Tipulidæ</i> spp. (Diptera)
<i>Glossiphonia complanata</i> (Hirudinea)	<i>Tabanidae</i> spp. (Diptera)
<i>Haemopsis sanguisuga</i> (Hirudinea)	

Phytophiles (associated with aquatic plants of all kinds).

<i>Polycelis nigra</i> (Tricladida)	<i>Elmis aeneus</i> (Coleoptera)
<i>Planorbis glaber</i> (Mollusca)	<i>Elmis volckmari</i> (Coleoptera)
<i>Canthocamptus staphylinus</i> (Copepoda)	<i>Helophorus viridicollis</i> (Coleoptera)
<i>Cyclops serrulatus</i> (Copepoda)	<i>Hydraena riparia</i> (Coleoptera)
<i>Asellus aquaticus</i> (Isopoda)	<i>Simulium reptans</i> (Diptera)
<i>Nemura standfussi</i> (Plecoptera)	<i>Sperchon glandulosus</i> (Hydracarina)
<i>Limnophilus decipiens</i> (Trichoptera)	<i>S. brevisstris</i> (Hydracarina)
<i>Anabolia nervosa</i> (Trichoptera)	<i>Megapus spinipes</i> (Hydracarina)
<i>Cranoecia irrorata</i> (Trichoptera)	<i>Lebertia</i> spp. (Hydracarina)
<i>Plectrocnemia conspersa</i> (Trichoptera)	<i>Hygrobatæ longipalpis</i> (Hydracarina)

B 2. Lower courses of longer rivers.

(a) *Gorge-sections.* The longer rivers, Rheidol and Ystwyth, after descending from the high plateau by cascades, pass through deep gorges in their middle courses: in these regions the river is a swift torrent cutting into the naked rock, or, in the wider sections of the gorges, it forms a shifting current sometimes split into parallel courses on a flood-plain of boulders and angular rock-fragments. The fauna bears some resemblance to that of the cascade-sections

of the plateau-streams, but with considerable reductions: practically the only types remaining are the stone-clingers, save in a very few places where eddies of relatively quiet water permit of the establishment of a few Algae and Bryophytes with their associated fauna. Characteristic species are:

True gorge association.

<i>Eodyurus lateralis</i> (Ephemerida)	<i>Rhyacophila oblitterata</i> (Trichoptera)
<i>Baëtis tenax</i> (Ephemerida)	<i>Hydropsyche angustipennis</i> (Trichoptera)
<i>Leuctra inermis</i> (Plecoptera)	<i>Dixa maculata</i> (Diptera)
<i>Isopteryx torrentium</i> (Plecoptera)	<i>Simulium latipes</i> (Diptera)
<i>Isogenus</i> sp. (Plecoptera)	<i>Planaria albissima</i> (Tricladida)

Occasional eddy association.

<i>Velia currens</i> (Hemiptera)	<i>Anacaena globulus</i> (Coleoptera)
<i>Plectrocnemia conspersa</i> (Trichoptera)	<i>Simulium reptans</i> (Diptera)
<i>Hydroporus rivalis</i> (Coleoptera)	<i>Tanytus nebulosus</i> (Diptera)
<i>H. Davisii</i> (Coleoptera)	

(b) *Plain-sections.* As mentioned above, the plain-sections of the courses of the longer rivers, although the gradient is much lower than in other reaches, have still a rapid current, and there is practically no really fine silt: the finest material brought down by the river in any quantity is rough grit, and any "mud" deserving of the name is derived *in situ* from the fluvio-glacial carpet of the lower valleys. Even this is largely covered by the extensive flood-deposits, which are remarkably copious and rough in character, owing to the presence of so many exposed mine-dumps near the streams in the hill-districts, which provide great quantities of broken rock-fragments all ready to be swept down by the river in its flood.

The "torrential" character is thus to a certain extent carried on practically to sea-level, and the fauna is predominantly of the lithophilous type, with the addition of a few limnophiles and phytophiles in quieter eddies where the fluvio-glacial mud provides the banks and immediate substratum.

The complete fauna list is practically a shortened version of that of the brooks of the coastal area; with the exception of the Sea-trout (*Salmo trutta*), a casual summer visitor, no single species has been found peculiar to these courses, save for a few definitely estuarine types, e.g. *Gammarus Duebeni* and *Notaspis lacustris*, occurring in the intertidal zone and not to be dealt with here. On the other hand, a good many species characteristic of the brooks are absent here. The majority of these are typical limnophiles and phytophiles, such as leeches, *Polycelis nigra*, and many Caddis-larvae, and their absence, like the scarcity of other types of similar habit, is no doubt directly related to the topographical conditions described above. But the complete absence of certain typical lithophiles is not so easily to be explained. The most interesting of the latter species are the Mollusc *Ancylus fluviatilis*, elsewhere so abundant in similar situations, and the two stone-loving Triclad, *Planaria alpina* and *Polycelis nigra*, whose distribution in this area will be dealt with later.

The general dearth of species in the lower rivers is not now, in the opinion

of the writer, to any extent referable to the chemical pollution caused by former lead-mining: a careful study of the conditions in the area ((12) to (16)) has shown that such pollution, marked by the introduction into the rivers of dissolved metallic salts, has not been renewed in the Lower Rheidol since the early months of 1924: since that date the waters have remained chemically pure, and a large influx of species has taken place into their area, but some other factor or factors (probably a combination of the lack of true silt and the acidity of the waters) have conditioned the relative poverty which still continues. In the case of Mollusca, absence or poverty of lime, and hydrogen-ion concentration as such, appear to play an important part in the elimination of species. Observations of the writer on the distribution of Molluscan species in the plateau region confirm the importance of relative acidity of the waters, and it has been shown by experiment that a low pH value, such as occurs in nature in some of the upland waters, is directly fatal to certain species, causing the rapid coagulation of mucus over exposed skin-surfaces (17).

IV. GENERAL CONSIDERATIONS AND COMPARISONS

A. List of animal species, with key to their distribution.

References explained in the text	Species	Group	Distribution in the Cardiganshire area		
			Streams of coastal area		
			Plateau streams	Spring brooks	Longer rivers
T B	<i>Hydra viridissima</i>	Hydrozoa	×	×	—
	<i>H. oligactis</i>	"	×	×	—
B R	<i>Polycelis nigra</i>	Tricladida	×	×	×
S T B	<i>Pol. cornuta</i>	"	—	×	×
	<i>Planaria albissima</i>	"	×	×	×
S T B	<i>Dendrocoelum lacteum</i>	"	×	×	×
S T B R	<i>Planaria alpina</i>	"	×	×	—
	<i>Sphaerium corneum</i>	Lamellibranchia	—	×	×
(S) (T)	<i>Pisidium nitidum</i>	"	—	×	—
(S) T B	<i>P. pusillum</i>	"	×	×	—
S (T) B	<i>Limnaea pereger</i>	Gastropoda	×	×	×
S (T)	<i>L. truncatula</i>	"	×	×	—
S T B	<i>Ancylus fluviatilis</i>	"	×	×	—
			frequent)		
(S) (B)	<i>Planorbis spirorbis</i>	"	—	×	—
	<i>Pl. albus</i> (?): (a dark-shelled variety)	"	—	×	×
(T) B	<i>Tubifex tubifex</i>	Oligochaeta	×	×	×
(T)	<i>Nais elinguis</i>	"	×	×	×
	<i>Stylaria lacustris</i>	"	×	×	—
	<i>Hirudo medicinalis</i>	Hirudinea	×	×	—
B	<i>Haemaphys sanguisuga</i>	"	×	×	—
T (B)	<i>Herpobdella octoculata</i>	"	×	×	—
(S) T B	<i>Glossiphonia complanata</i>	"	×	×	—
S B	<i>Helobdella stagnalis</i>	"	—	×	—
B R	<i>Cyclops serrulatus</i>	Copepoda	×	×	×
	<i>Cy. prasinus</i>	"	—	×	—
S B	<i>Cy. fimbriatus</i>	"	—	×	×
B	<i>Cy. fuscus</i>	"	×	×	—
(S) R	<i>Canthocamptus minutus</i>	"	—	×	—
B R	<i>Ca. staphylinus</i>	"	—	×	—
	<i>Eurycerus lamellatus</i>	Cladocera	×	×	×
S	<i>Chydorus sphaericus</i>	"	—	×	—
B	<i>Cypris virens</i>	Ostracoda	×	×	—
S	<i>C. fuscata</i>	"	—	×	—

References explained in the text	Species	Group	Distribution in the Cardiganshire area.		
			Streams of coastal area		
			Plateau streams	Spring brooks	Longer rivers
(S) B	<i>Herpetocypris reptans</i>	Ostracoda	x	x	—
S T B R	<i>Gammarus pulex</i>	Amphipoda	—	x	—
S T B R	<i>Asellus aquaticus</i>	Isopoda	x	x	—
(S) (T) B	<i>Hygrobatas longipalpis</i>	Hydracarina	—	x	—
S (T) B	<i>Sperchon glandulosus</i>	"	x	x	x
(S) (T)	<i>Sp. brevirostris</i>	"	—	x	—
(T) (B)	<i>Megapus spinipes</i>	"	—	x	—
	<i>Limnesia koenikei</i>	"	—	x	—
(S) (T) (B)	<i>Lebertia</i> sp.	"	x	x	—
S	<i>Podura aquatica</i>	Collembola	x	x	x
S	<i>Isotomurus palustris</i>	"	x	x	x
	<i>Hydrometra stagnorum</i>	Hemiptera	x	x	—
(B)	<i>Gerris najas</i>	"	—	x	x
B	<i>G. gibbifera</i>	"	x	—	—
B	<i>Velia currens</i>	"	x	x	x
B	<i>Notonecta glauca</i>	"	—	x	x
	<i>Sigara minutissima</i>	"	—	x	x
(B)	<i>Corixa limitata</i>	"	x (rare)	x	x
(S) (T)	<i>Dictyopteryx mortoni</i>	Plecoptera	—	x	x
	<i>Perla</i> sp.	"	x	—	—
(S) (T)	<i>Isogenus</i> sp.	"	x	—	—
(T) (B)	<i>Leuctra inermis</i>	"	x	x	x
S (T)	<i>Isopteryx torrentium</i>	"	x	x	x
S T (B)	<i>Nemura standfussi</i>	"	x	x	x
(S)	<i>Nephelopteryx</i> sp.	"	x	—	—
	<i>Siphonurus lacustris</i>	Ephemera	x	x	x
	<i>S. armatus</i>	"	x	—	—
(S) (T) (B)	<i>Baëtis tenax</i>	"	x	x	x
(S) (T) (B)	<i>B. vernalis</i>	"	x	—	—
(S) (T) (B)	<i>Ecdyurus lateralis</i>	"	x	x	x
	<i>Ischnura elegans</i>	Odonata	x	x	—
	<i>Platycnemis pennipes</i>	"	—	x	x
	<i>Libellula quadrimaculata</i>	"	—	x	—
(B)	<i>Agrion pulchellum</i>	"	—	x	—
	<i>Cordulegaster annulatus</i>	"	—	x	x
T B	<i>Sialis flavilatera</i>	"	—	x	x
(S) T (B)	<i>Rhyacophila obliterata</i>	Trichoptera	x	x	x
S T B	<i>Agapetus fuscipes</i>	"	x	x	x
T	<i>Philopotamus montanus</i>	"	x	x	—
(T) (B)	<i>Silo nigricornis</i>	"	x	x	—
S T B R	<i>Crunoecia irrorata</i>	"	—	x	x
(T)	<i>Brachycentrus subnubilus</i>	"	—	x	—
(S) T B	<i>Apatania fimbriata</i>	"	x	—	—
(T)	<i>Dipletrona felix</i>	"	—	x	—
T	<i>Hydropsyche angustipennis</i>	"	x	x	x
(S) T	<i>Plectrocnemia conspersa</i>	"	x	x	x
(S)	<i>Cyrtus insolutus</i>	"	x	x	x
T B	<i>Anabolia nervosa</i>	"	x	x	x
(T)	<i>Limnophilus decipiens</i>	"	x (rare)	x	x
(T) (B)	<i>L. flavicornis</i>	"	—	x	—
(T) B	<i>L. bipunctatus</i>	"	x	x	—
B	<i>Glyptohaelius pellucidulus</i>	"	—	x	—
(T) B	<i>Mesophylax impunctatus</i>	"	x	x	x
B	<i>Halesus digitatus</i>	"	x	—	—
B	<i>Dytiscus marginalis</i>	Coleoptera	x	(rare)	x
	<i>Laccophilus interruptus</i>	"	—	x	x
(S) (T) B	<i>Agabus bipustulatus</i>	"	x	x	—
(S) (T) B	<i>A. paludosus</i>	"	x	x	—
(S) (T)	<i>A. chalconotus</i>	"	x	x	—

References explained in the text	Species	Group	Distribution in the Cardiganshire area		
			Plateau streams	Streams of coastal area	
				Spring brooks	Longer rivers
T	<i>Platambus maculatus</i>	Coleoptera	x	x	—
(S) T	<i>Hydroporus rivalis</i>	"	x	x	x
(S) (T)	<i>H. Davasii</i>	"	x	x	x
(S) (T) (B)	<i>H. obscurus</i>	"	x	—	—
(S) (T)	<i>H. pubescens</i>	"	x	—	—
	<i>Deronectes latus</i>	"	—	x	—
	<i>D. depressus</i>	"	—	x	x
T B	<i>Gyrinus natator</i>	"	x	x	x
	<i>Hydrophilus caraboides</i>	"	—	x (rare)	—
(S) T B	<i>Limnebius truncatellus</i>	"	x	x	—
T (B)	<i>Hydraena riparia</i>	"	—	x	—
(T) (B)	<i>Helophorus viridicollis</i>	"	x	x	—
T B	<i>Elmis volckmari</i>	"	x	x	—
(T)	<i>E. aeneus</i>	"	x	x	x
	<i>Limnius tuberculatus</i>	"	—	x	—
	<i>Cercyon</i> sp.	"	—	x	—
(S) T B	<i>Anacaena globulus</i>	"	x	x	x
	<i>Theobaldia annulata</i>	Diptera	—	x	—
(B)	<i>Trichocera regelationis</i>	"	—	x	—
(T)	<i>Orthocladus stercorarius</i>	"	—	x	x
(T) (B)	(<i>Culicidae</i> spp.)	"	x	x	x
(S) (T) (B)	<i>Tanytarsus flavipes</i>	"	—	x	—
(S) (T) (B)	<i>T. vernus</i>	"	—	x	—
(S) (T)	<i>Chironomus</i> sp. (plumosus-group)	"	x	x	x
(S)	<i>Ch.</i> spp. (other groups)	"	—	x	—
(S)	<i>Ceratopogon</i> sp.	"	—	x	—
(S)	<i>Metriocnemus</i> sp. (? <i>fuscipes</i>)	"	—	x	—
	<i>Tanytus nebulosus</i>	"	x	x	x
(S) T (B) R	<i>Dixa maculata</i>	"	x	x	—
(S) (T) (B)	<i>D. nebulosa</i>	"	—	x	—
T R	<i>Orphnephila testacea</i>	"	x	—	—
S T B R	<i>Pericoma canescens</i>	"	x	x	—
(S) (T) (B)	<i>Simulium latipes</i>	"	x	x	x
(S) (T) (B)	<i>S. reptans</i>	"	x	x	x
	<i>Eristalis</i> sp. (? <i>tenax</i>)	"	—	x	—
(S) (T) (B)	<i>Tabanidae</i> sp. (? <i>Atylotus</i> sp.)	"	—	x	x
(S) (T) (B)	<i>Tipulidae</i> spp.	"	x	x	—
	<i>Gastrosteus aculeatus</i>	Pisces	—	x	x
	<i>Anguilla vulgaris</i>	"	—	x	x
T	<i>Leuciscus phoxinus</i>	"	x	x	—
T	<i>Salmo fario</i>	"	x	x	x
	<i>Triton palmatus</i>	Amphibia	x	—	—
(S)	<i>Rana temporaria</i>	"	x	x	x

Reference to the right-hand columns of the above table, which supply the key to distribution within the Cardiganshire area, shows that, with the rarest exceptions, practically every species occurring on the High Plateau (above the 900-foot contour-line) is also to be found in streams of the lower coastal area. The exceptions are so few that they can be enumerated singly: the most remarkable is the newt *Triton palmatus*, and beyond this only a few Insect-species are to be mentioned:

Gerris paludum (Hemiptera)
Nephelopteryx sp. and *Isogenus* sp. (Plecoptera)
Siphonurus armatus and *Baëtis vernus* (Ephemera)
Apatania fimbriata and *Halesus digitatus* (Trichoptera)
Hydroporus obscurus and *H. pubescens* (Coleoptera)

On the other hand, a larger number of species occur in the coastal brooks which are absent from those of the Plateau: these are mainly phytophilous and limnophilous larvae of Trichoptera, Odonata and Diptera. The chief distinction between the high and low areas as regards general biocoenotic type is thus seen to be dependent on "limnocene" or "rheocene" character rather than upon factors more directly related to elevation and range of temperature.

Comparisons of a different kind are indicated by the symbols appearing in the left-hand column, preceding the names of animal-species. The symbols here refer to species collected by continental workers on streams of European highlands: S refers to the list compiled by Steinmann (9) from his study of mountain brooks of glacial origin in the Jura, the Schwarzwald, the Alps and the Karst; T to Thienemann's lists, compiled from studies of brooks of the Westphalian Sauerland, at an elevation of 250 to 550 metres (1), of Baumberg, West of Münster (1), and of the Jasmund peninsula of the Island of Rügen (2); B to those of Bornhauser, from collections made in the neighbourhood of Basel (6); and R to a list given in a much slighter study, by Demel, of post-glacial rheocenes contributing to Lake Wigry in Poland (7). A bracketed symbol, thus—(S)—indicates that not the actual species in question, but some species closely allied to it, is named; apart from such cases, of the species collected by the writer:

19 are identical with Steinmann's species;

32 with Thienemann's;

42 with Bornhauser's; and

11 with Demel's.

These figures should serve to establish a certain similarity in general type between the present field of research and those of the earlier studies. In addition, certain species occur, and occur generally, in this area, which have been definitely established by continental workers as belonging to the stenothermous, torrenticolous group representing the true primitive fauna of mountain brooks, and probably to be classed as "glacial relicts," in contradistinction to the large number of "eurythermous" types, mostly dwelling in mud, sand, or plant-growth, and insurgent into the highland brooks by migration along the slower waters of the plains. The most definitely "stenothermous" types found in the Cardiganshire area are:

<i>Planaria alpina</i> (Tricladida)	<i>Agapetus fuscipes</i> (Trichoptera)
<i>Polycelis cornuta</i> (Tricladida)	<i>Rhyacophila obliterata</i> (Trichoptera)
Certain <i>Hydracarina</i>	<i>Crunoecia irrorata</i> (Trichoptera)
<i>Apatania fimbriata</i> (Trichoptera)	<i>Plectrocnemia conspersa</i> (Trichoptera)

and these are (with one exception—*Apatania fimbriata*) quite as general in occurrence in the lowland brooks as on the plateau. It is maintained, therefore, that practically the whole of the streams of this area may be classed as of the type of "mountain brook," of torrential character and partly peopled, in relation to the consistently low temperature and rapid streaming of their waters, by fauna representing relicts of former glaciation. In this connection,

a special reference must be made to the Turbellaria-Tricladida of the neighbourhood.

In the first place, *Planaria gonocephala*, a "eurythermous cosmopolitan" common in the continental and also in certain British areas (18), does not occur here at all. The distribution of this species is undoubtedly related to the lime content of the streams: Bornhauser (6) has noted its absence from soft waters, and there appears little doubt that its failure to occur in the Cardiganshire area is related to the prevalent scarcity of lime. Two other eurythermous species, common in Britain and elsewhere, are found here, *Polycelis nigra* on plant growth in streams of the limnocrene type, and *Dendrocoelum lacteum* in somewhat similar situations and especially where pollution from house-drainage, cattle fouling, etc., eliminates other Triclad species. The commonest and most tolerant of widely varying conditions is *Planaria albissima* Vejd. (17a), a species never before recorded from any British area, yet to be found here in practically every body of running water in the district, highland and lowland, rheocrene and limnocrene, small trickle and larger river, alike. Sometimes it is the only Triclad in a particular reach, at other times it occurs side by side with *Planaria alpina* and *Polycelis cornuta*: from its general occurrence in situations so diverse in character, there seems good reason to describe it as "eurythermous, ubiquitous and probably cosmopolitan." Vejdovsky (33) found it in spring brooks in Bohemia: none of the writers whose studies of mountain brooks in European districts have been quoted appear to have found it, and Steinmann, in a passing note (9) refers to it as "a rare species."

The two remaining species, *Planaria alpina* and *Polycelis cornuta*, are of very particular interest in ecological study: they are the classic examples of "glacial relicts" in the brook-fauna, and much literature has accumulated around the study of their distribution and bionomics ((19) to (32)). In general, *Planaria alpina* frequents the upper reaches of streams of European highlands, *Polycelis cornuta* the middle, and *Planaria gonocephala* the lower, the habitats to some extent overlapping; *Planaria alpina* is a markedly stenothermous type, *Polycelis cornuta* has its optimum temperature slightly higher; the former is associated with hard waters rich in lime, the latter with soft waters. To these general rules, well established by continental workers, the special distribution of the two Alpine species in Cardiganshire does not altogether conform. In the first place, as already noted, the lime content is usually very low, yet *Planaria alpina* is distinctly more widely distributed than *Polycelis cornuta*, nor is the former species absent from brooks with lime content so low as even 2.5 mg. per litre. Secondly, the distribution as regards height is by no means typical, since individuals occur in greater numbers in the low coastal region than on the plateau, and *Planaria alpina* occurs at a lower level, in some cases, than *Polycelis cornuta*. Thirdly, the distribution is "patchy" in the extreme, and since its peculiar features cannot be altogether explained by the recognised rules, it appears that some other biological factor

must be sought. Further comment is withheld for the present, as a detailed investigation of the problem is now in process.

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A PRELIMINARY ACCOUNT OF THE VEGETATION OF THE RIVER ITCHEN

By R. W. BUTCHER

(*With two Figures in the Text.*)

INTRODUCTION

THE following account of the vegetation of a stream in the South of England is based on observations made during 1925 at the Ministry of Agriculture and Fisheries Freshwater Station, Alresford, as a preliminary to a full biological survey of the river system. The general object of such a survey is to form a comprehensive idea of all the biological conditions in a typical unpolluted river, and further to compare such results with the life in polluted streams so as ultimately to use the absence or presence of certain organisms to indicate the state of purity of river waters throughout England (cf. Kolkwitz and Marsson (5)). It is surprising that the ecology of streams has attracted so little attention. There are, of course, numerous papers on the phytoplankton of larger rivers, notably those of Kofoed (4) in America and of Schröder (10), Limanowska (6), etc., on the continent, but the biology of smaller streams would appear to have been almost entirely neglected, not only from the point of view of the phanerogamic flora but from that of the algal vegetation also. Because of this lack of work on the subject it was considered advisable to present these short notes.

TOPOGRAPHY

The River Itchen rises near Cheriton and is about 30 miles in length. The land drained by the river system consists mainly of a gravelly loam lying in the Upper Chalk.

In ancient times the Itchen was a series of swamps and marshes rather than a river. The Romans and the Saxons carried out a certain amount of drainage, but it was that able bishop, Godfrey de Lucy (*circa* 1220), who drained swamps and deepened the channels of the Alre and the Itchen, so making it navigable from Alresford to the sea. Vestiges of his work still remain between Alresford and Winchester, and below Winchester the canal was used until quite recent times.

As a river system it is somewhat complex; there are numerous channels that drain the water meadows and in many places (for instance, at Itchen Abbas) the water level is higher than the surrounding marshes. Without attention, the river system would probably degenerate into its primeval state of swamp and pools. The numerous channels make it difficult to carry out an exhaustive survey or to translate the results into any but general terms.

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CHEMICAL COMPOSITION OF THE WATER

Below is the average chemical composition of the River Itchen at Alresford.

Total solids	CaO	Oxygen absorbed	CO ₂	Cl ₂	SiO ₂	NO ₃	pH
30.2	12.94	0.027	0.5	1.3	0.4	0.41	8.0

(In parts per 100,000.)

As the above figures suggest, the stream is capable of supporting a large fauna and flora; the bed of the stream is everywhere covered with vegetation. *Gammarus*, molluscs and insect larvae are abundant and the river is well known for its excellent trout.

GENERAL CHARACTER OF THE FLORA

The course of the river may be divided into four parts according to the flora. A general plan of the first, second, and part of the third portions, which were particularly surveyed, together with the dominant species of plants, is given in Fig. 1.

(a) *From the source to Martyr Worthy.* In this portion *Ranunculus penicillatus*, *Apium nodiflorum* and *Sium angustifolium*, with *Nasturtium officinale* near the banks are the chief plants. The banks are very low and ill-defined and the river in many places tends to have swampy margins. There is an abundant littoral flora of *Sparganium erectum*, *Carex paludosa*, *Carex paniculata*, *Glyceria aquatica*, *Typha latifolia*. *Hippuris vulgaris* and *Sparganium simplex* are subdominant in some of the lower portions of this stretch.

(b) *From Martyr Worthy to Kings Worthy.* *Hippuris vulgaris* and *Sparganium simplex* here become more common and *Elodea canadensis* and *Callitriche stagnalis* are dominant in some stretches. The banks are well above the level of the river and there is little littoral growth; *Phragmites communis* is the commonest "reed" in this portion.

(c) *Between Kings Worthy and Bishopstoke.* *Elodea canadensis* and *Callitriche stagnalis* are frequently dominant in this portion, but *Hippuris vulgaris* and *Sparganium simplex* are still common. *Ranunculus penicillatus* and *Sium angustifolium* are met with here in swift stretches.

(d) *Between Bishopstoke and the Estuary.* Here the river is deep and often turbid, so that complete observation of the vegetation is difficult. *Elodea canadensis* and *Callitriche stagnalis* are the dominant plants and *Sium angustifolium*, *Hippuris vulgaris* and *Oenanthe fluviatilis* are occasionally seen.

There is naturally no well-marked line of demarcation between these sections, and (b) and (c) are really only transition-regions between (a) and (d). Plants notably absent in the river system are: water lilies, all species of Alismaceae, *Ceratophyllum*, *Utricularia* (which occurs in the neighbouring River Test) and Characeae.

The following table gives a summary of the dominant species in the

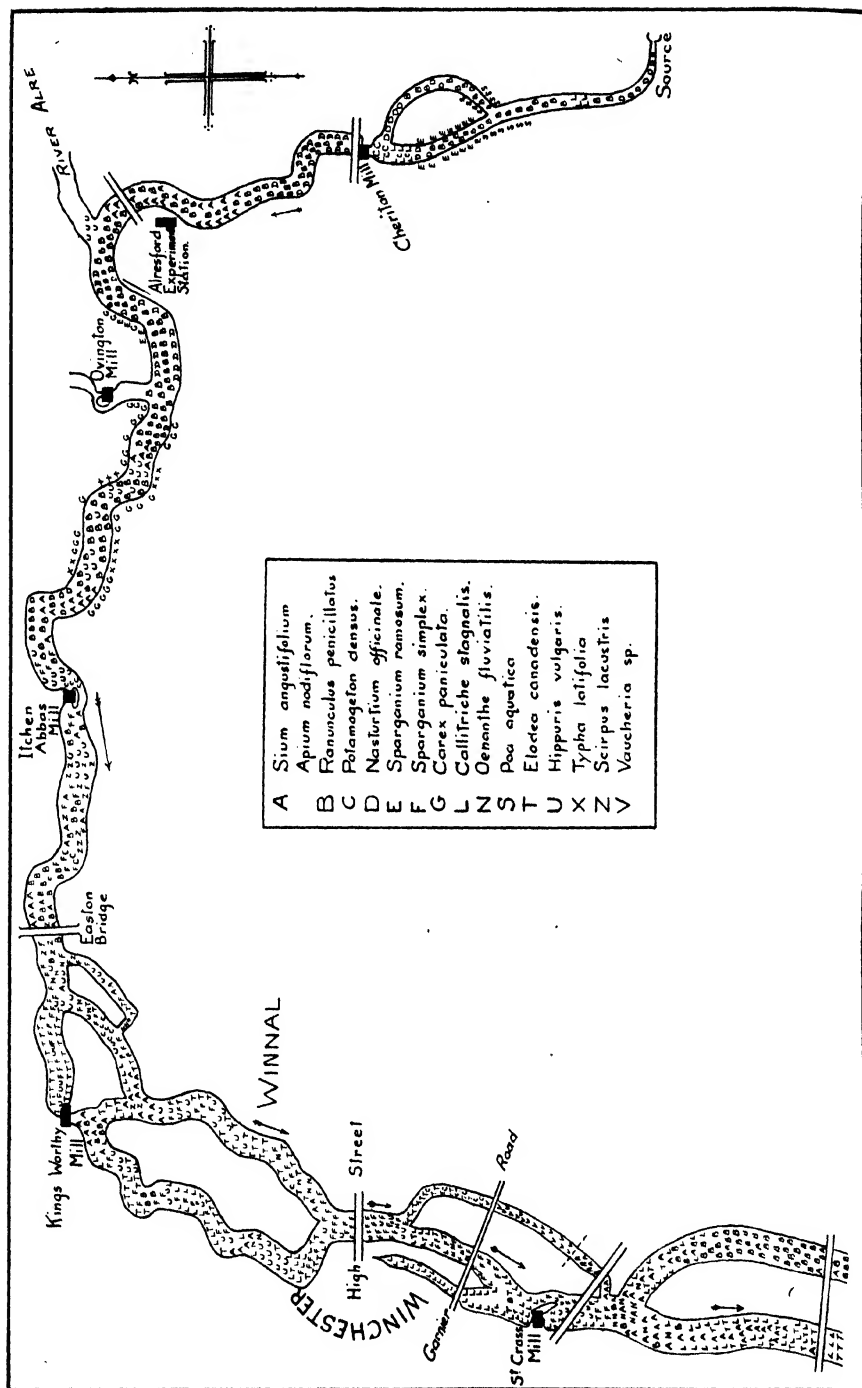


FIG. 1. Diagram of the course of the Itchen from the source to Twyford showing dominant Phanerogams of the river beds. General scale about 1 inch to the mile. Width of stream beds greatly exaggerated.

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different stretches. From this it will be seen that there is correlation in at least five out of the eight species with rate of flow and nature of bed.

Dominant species of different stretches of the River Itchen, in order of fall of bed and rate of flow.

Stretch of river	River bed	Approx. distance from source miles	Fall in feet per mile	Approx. speed of flow m.p.h.	Dominant species
Source to Cheriton Mill	Large and small stones	0-2	20	2½-3½	<i>Apium nodiflorum</i>
N. of Winchester to S. of Win- chester	Small stones	12.7-14	15	1½-2½	<i>Oenanthe fluviatilis</i> <i>Sparg. simplex</i>
Cheriton Mill to Alresford	Large and small stones	2-4.2	12	1-2	<i>Apium nodiflorum</i>
Alresford to Ovington Mill	Small stones	4.2-4.8	12	1-2	<i>Ranunculus penicillatus</i>
Ovington Mill to Itchen Abbas	Small stones and sandy	4.8-7.2	11.6	1-2	<i>Sparganium simplex</i> <i>Hippuris vulgaris</i>
St Cross Mill to Twyford	Small stones and gravel	14.5-16.9	10	0.75-2	<i>Sium angustifolium</i>
Itchen Abbas to Kings Worthy	Small stones and sandy	7.2-10.5	7.2	0.5-1.5	<i>Elodea canadensis</i>
Twyford to Allbrook	Gravelly	16.9-19.4	6.6	0.5-1.5	<i>Callitriche stagnalis</i>
Allbrook to Bishopstoke	Gravelly	19.4-21.9	6.6	0.5-1.5	
Kings Worthy to N. Winchester	Gravelly to muddy	10.5-12.7	6.0	0.5-1.5	
S. Winchester to St Cross Mill	Muddy	14.0-14.5	4.0	0.25-1.0	
Bishopstoke to Wood Mill	Muddy	21.9-24.4	4.5	0.25-1.0	

RELATIONSHIP OF VEGETATION TO PHYSICAL CONDITIONS

(1) *Deposition of Silt.* It has been shown by Pearsall (9) that silting has a marked effect upon the vegetation of the English lakes. The same is equally true of a river, but conditions under which silt is deposited are somewhat

different. It is obvious that at different velocities materials may be carried whose masses are proportionate to the flow of the current.

Velocity	Nature of river bed
Above 4.0 ft. per sec.	Stratified rock
„ 3.0 „	Heavy shingle
„ 2.0 „	Light shingle and pebbles
„ 1.0 „	Light gravel
„ 0.67 „	Sand and silty beds
„ 0.42 „	Clay beds
Below 0.42 „	Alluvial deposits

These figures are taken from Minikin's *Practical and Canal Engineering* (7) and are confirmed by observations made at Alresford on the River Itchen. Owing to almost infinite variations, actual observations on the speed of flow of the River Itchen throughout its length have not been carried out, but there is given on p. 58 the average fall per mile of the river taken from the 6-inch Ordnance Survey Map. It can be seen from this table that the plant communities change where there is a marked change in the current.

Reference to the plan of the river (Fig. 1) shows that in the stretch between Winchester and St Cross, the two typical silt-loving plants (*Callitriche* and *Elodea*) are dominant. The same applies, to a less marked extent, in a stretch between Easton Bridge and Winnall, particularly at the mill weirs and hatches.

The stretches below Twyford apparently show the same phenomenon, but the vegetation has not been thoroughly investigated here. Plants that appear to prefer a moderate amount of silt and dominate many of the moderately slow portions of the river are *Sparganium simplex*, *Hippuris vulgaris* and *Oenanthe fluviatilis*. On the other hand, *Ranunculus penicillatus* and *Sium angustifolium*, and to a less extent *Ranunculus fluitans*, become dominant in the swiftly flowing parts, the first being particularly abundant between Cheriton and Ovington.

Watson (11), in a paper devoted chiefly to mosses and lichens of waters, but in which he also mentions some of the Phanerogams, similarly divides the types of vegetation of what he describes as the submerged community into quickly and slowly flowing water, but, contrary to his statement, the quickly flowing parts of the Itchen are very poor in Bryophytes and certain flowering plants are abundant. The northern streams mentioned are liable to become very low in the dry season and the rocks on which the Bryophytes grow are exposed and they become similar to rocks watered by the spray of a cascade or by small trickles and are scarcely to be compared with stones that are permanently submerged. This exposure of the rocks and stones, rather than the actual aeration of the water, is the probable cause of the difference in the Bryophytic vegetation of permanently and temporarily submerged rocks.

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The following are the plant communities of the silted, partly silted and non-silted portions:

Silted.

<i>Elodea canadensis</i>	d	<i>Callitriche stagnalis</i>	sd
<i>Hippuris vulgaris</i>	a	<i>Sparganium simplex</i>	a
<i>Oenanthe fluviatilis</i>	f	<i>Potamogeton pusillus</i>	f
<i>Potamogeton crispus</i>	r	<i>Potamogeton densus</i>	r
<i>Ranunculus fluitans</i>	r	<i>Vaucheria</i> sp.	o

Partly silted.

<i>Hippuris vulgaris</i>	sd	<i>Sparganium simplex</i>	sd
<i>Oenanthe fluviatilis</i>	a	<i>Scirpus lacustris</i>	a
<i>Elodea canadensis</i>	f	<i>Callitriche stagnalis</i>	f
<i>Potamogeton densus</i>	f	<i>Potamogeton crispus</i>	o
<i>Lemna trisulca</i>	o	<i>Ranunculus fluitans</i>	o
<i>Ranunculus penicillatus</i>	o	<i>Apium nodiflorum</i>	o
<i>Sium angustifolia</i>	o	<i>Typha latifolia</i>	o

Non-silted.

<i>Ranunculus penicillatus</i>	d	<i>Apium nodiflorum</i>	sd
<i>Sium angustifolium</i>	sd	<i>Potamogeton densus</i>	a
<i>Fontinalis antipyretica</i>	a	<i>Nasturtium officinale</i>	a
<i>Veronica anagallis</i>	f	<i>Mimulus Langsdorffii</i>	o
<i>Oenanthe fluviatilis</i>	o	<i>Cladophora</i> sp.	o

d = dominant, sd = subdominant, a = abundant, f = frequent, o = occasional, r = rare.

It is evident that depositions of silt form easy germinating and rooting positions for plants. This fact alone will account for a longer list of occasional plants in the silted and partly silted areas. It also leads indirectly to the consideration of the second factor affecting distribution.

(2) *Anchoring power of the roots.* All plants in running water are subject to the stress of water-flow and their ability to grow in a given area is partly dependent on the anchoring power of their roots. For instance, *Elodea* and *Callitriche* have an anchoring system of filamentous, adventitious roots and weak stems that are easily washed away in flood periods. Rootless plants such as *Lemna* only exist in very slow flowing water or tangled in littoral vegetation. The root systems of *Ranunculus penicillatus* and *Potamogeton densus* consist of thick rhizomes and intertwining roots that grow down between the stones and thus secure a very powerful hold. Such roots will account for the comparative abundance of silt-loving plants like *Scirpus lacustris* in several swiftly flowing portions of the stream. The chief problem of survival is whether the seeds or winter buds of such plants can successfully germinate. Under the same category can also be included the strength of stems and leaves. The brittleness of the Characeae will account for these plants never growing in any but still waters. The bottom algal flora shows the same distribution. Diatoms are abundant in the Itchen and can frequently be seen as brown patches on the mud and stones or as fluffy growths on other plants. In the swift portions filamentous forms such as *Melosira varians*, *Diatoma vulgare*, pedicelled forms such as *Cymbella* spp., *Gomphonema* spp., and forms with mucilaginous sheaths such as *Cocconeis placentula* are the most abundant. In the slower portions

there is a much greater variety; *Gyrosigma attenuatum*, *Synedra* spp., *Nitzschia* spp., being very abundant.

(3) *Sunlight*. The effect of shade on the distribution of plants on land is well known. There is a similar effect with water-plants though not so well marked. The chief shade-plant of the Itchen is *Sium angustifolium* and it can be frequently observed as growing furthest under bridges, tunnels and the like.

Fig. 2 shows the effect of shade on certain of the river species very clearly. It will be seen that *Ranunculus penicillatus* diminishes in quantity and *Sium angustifolium* increases, in the shady portions. The light is never fully cut off, though under the railway bridge there is hardly ever any direct sunlight.

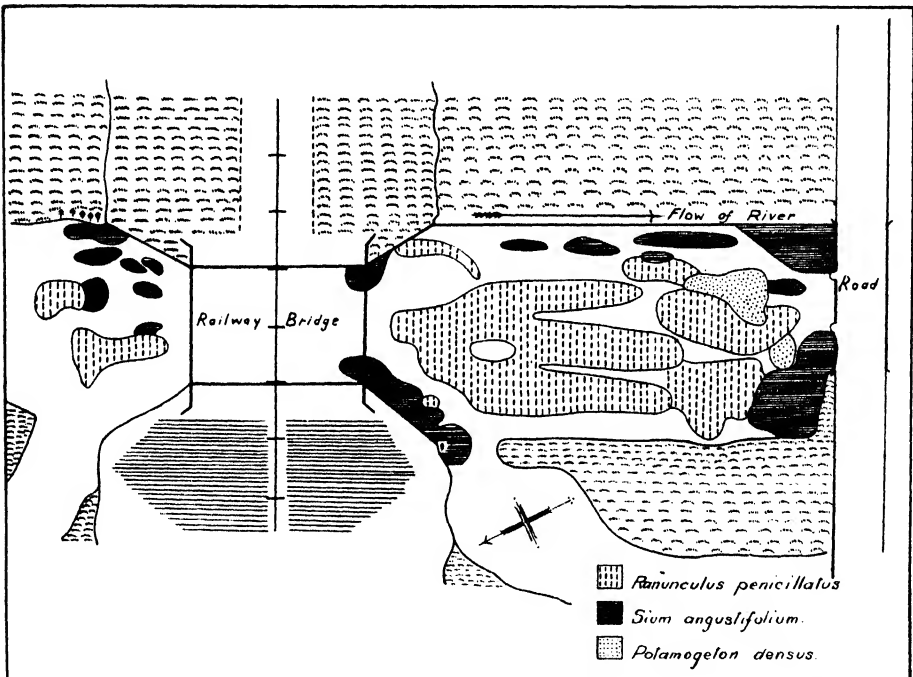


FIG. 2. Diagram of the distribution of three species of aquatic Phanerogams in the vicinity of two bridges crossing the Itchen, showing the effect of shading.

(4) *Chemical constituents of the water*. The general composition of the water has been given above, but it is possible that changes in different parts of the river may account for changes in vegetation. The difficulties of estimating some of the constituents (such as alkalies) mean that these figures are very incomplete.

Aeration. The two gases dissolved in water which are of any significance to plant life are oxygen and CO_2 . The conditions of aeration in the water are very different from those on land. Whereas the CO_2 in the air is often a limiting factor in plant nutrition, this is not so in the water, because the proportion

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and amount of CO₂ is greatly increased. Further, Brown (2) shows that not sufficient CO₂ diffuses from the air to keep *Elodea* alive during winter and spring, so that this difference must be made up from the CO₂ in the water and that given off from the mud, presumably fixed in the form of bicarbonates. Figures of amounts for the River Itchen confirm those of other writers (Devaux (3) and Arber (1)).

	Air (c.c./litre, N.T.P.)	River Itchen (c.c./litre, N.T.P.)
Oxygen	200	7.0
CO ₂	0.3	2.55

From the above figures it will be seen that there is an abundance of CO₂, and it would seem from a knowledge of the gas requirements of plants in general that the small changes in concentration in different parts of the river will not influence the change of vegetation.

As regards oxygen, there is evidently a shortage as compared with the atmosphere even in the most ideal waters. The River Itchen is super-saturated in respect of oxygen. When the water flows over a weir or gets similarly stirred up the oxygen approximates to saturation point. It never happens, however, that the conditions at the bottom of a weir are the same as those above, for as well as this change in oxygen concentration, silt deposition and churning and stressing effects on the plants must also come in. The only noticeable change in the vegetation is the abundance of *Potamogeton densus* below most weirs and hatches, but this occurs in quantities elsewhere and does not appear to be dependent on the change in aeration mentioned above.

Calcium. The Itchen flows over chalk for almost the whole of its length and has therefore a high calcium content. Several samples were taken at different parts of the river on the same day to find out whether there was any variation. The results were as follows:

Locality	CaO in parts per 100,000
Alresford Experimental Station	13.02
Itchen Stoke Bridge	13.02
Ovington Mill	12.76
Chilland	12.46
Worthy Mill	12.6
Worthy Down	12.46
Winnall	12.6
Canal below Winchester ...	12.32
St Cross Mill	12.04

It will be seen that there is a progressive decrease in calcium content from source towards the mouth of the river, but, owing to the high amounts present everywhere, not sufficient to bring about any change in vegetation. There seems little doubt that the high calcium content of the river is responsible for the characteristic and abundant vegetation throughout the system.

Further investigations are being carried out as to the effects of phosphates,

nitrates and silica on the vegetation, but as yet sufficient data have not been obtained to enable any definite conclusions to be drawn.

Perennation of water-plants. One of the most notable features of the vegetation of the river, also mentioned by Arber (1), is the fact that it does not die down in the winter months. A patch of vegetation has been under observation at Alresford since last July, and the area occupied by the respective plants is still the same six months after, though the quantity per unit area has decreased somewhat. In the submerged water-plants mentioned in this paper there are, as far as can be ascertained, no exceptions. *Elodea*, *Callitriche* and other plants growing in the silted stretches get washed away to a large extent during winter floods, but the remnants continue to grow or at least to remain green.

NOTES ON THE SPECIES THAT MAKE UP THE FLORA OF THE RIVER

Batrachian Ranunculi—only two species have been observed in the Itchen. *Ranunculus penicillatus* Babington = *R. pseudo-fluitans* Baker and Foggitt, is very abundant, but never with floating leaves. It is confined almost entirely to the swift and sunny portions of the river and occurs in almost pure colonies at Ovington and Tichborne. *Ranunculus fluitans* has been observed, in small quantity only, at Winchester, Twyford and Bishopstoke.

Apium nodiflorum Reich fil. and *Sium angustifolium* L. These two plants (locally known as water celery) are difficult to discriminate as normally they do not flower. Apparently the former is commoner in the reaches above Alresford and only the latter occurs below Kings Worthy. There are very few places without plants of these species and in shady places, one or the other is frequently dominant. They attain their best development in swift reaches which are therefore free from silt.

Oenanthe fluviatilis Coleman. This plant occurs in small patches in the lower reaches of the river. It flowers only close to the bank in sluggish parts. It apparently grows best in deep water, direct sunlight and a moderate amount of silt. No plants have been observed above Martyr Worthy (halfway between Ovington and Easton Bridge).

Hippuris vulgaris L. This occurs in quantity in the deeper parts of the river and where there is a moderate current and a moderate amount of silt. Aerial flowering stems are produced in the slower portions of the river. It flourishes best in direct sunlight and a moderate amount of silt.

Callitriche stagnalis Scop. In the river this occurs where there are large amounts of silt, especially near the river banks, and seems to flourish better in shady places than in direct sunlight. It is dominant in the very silted stretch between Winchester and St Cross. The segregate species are not determinable, as the plant seldom flowers in the river. Although, like most of the water plants, it is constantly growing, large amounts get washed away with silt in flood periods.

Elodea canadensis Michx. Together with the last this is the dominant silt-

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inhabiting species. It grows only where there are large amounts of silt and is very conspicuous in the canal below Winchester. The plant also suffers in the same way as *Callitriche* during flood periods as it gets broken up and washed away.

Sparganium erectum L. This occurs as an erect rooted plant in the highest reaches of the river from the source to Ovington. It grows chiefly near the banks, where there is not too vigorous a current and a moderate amount of silt.

Sparganium simplex Huds. This species, locally known as ribbon-grass, is one of the subdominant plants in the swiftest stretches below Itchen Abbas. The plants do not flower except in small land-locked puddles at the side and are usually totally submerged. It appears to maintain itself in swifter stretches by the anchoring power of its roots and the lack of resistance of its leaves. The colonies are probably augmented from seeds that can germinate successfully from flowering specimens in backwaters and ditches.

Scirpus lacustris L. This species, though usually associated with lakes and sluggish stretches of rivers, occurs in some quantity in the swifter stretches of the River Itchen. It can probably maintain itself in these places like the last species because of the anchoring power of its roots.

Potamogeton densus L. Dominant in one or two small portions of the river. It appears to be associated with the swifter portions and also with hatches or weirs, both just above and below the fall of the water. It is difficult to explain its occurrence with our present defective knowledge of conditions in the river.

SUMMARY

1. A preliminary account is given of the flora of the River Itchen, particular attention being paid to the Phanerogamic flora.

2. Of all the environmental conditions examined affecting the nature of the flora that of deposit of silt appears to be the most important. Other factors are anchoring power of roots, sunshine, and perhaps chemical composition of the water, though not many observations have been made on this point.

3. The plant communities can be divided into silted, partly silted and non-silted types.

4. The chief plants of the river are dealt with in detail in respect of their habitats.

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FACTORS AFFECTING ANIMAL DISTRIBUTION IN A SMALL STREAM OF THE PANAMA RAIN-FOREST IN THE DRY SEASON¹

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(With two Figures in the Text.)

SHANNON CREEK flows down a steep V-shaped ravine on the north side of Barro Colorado Island into Gatun Lake, passing just east of the Laboratory of the Institute for Tropical Research. During the dry season in 1924 water stood in pools along the lower 200 yards. There was a slight permanent flow for half this distance. The whole gradient is steep, particularly so near the lake where the stream falls some 30 ft. in its last 50 ft. of horizontal flow. About a hundred yards above, there are similar rapids. Aside from these places the gradient is steady with a total fall of about 90 ft. in the region studied. Thirty-six pools were investigated, comprising all the pools in the upper part of the stream and the larger ones below. They will be referred to in their ordinal number from Gatun Lake. The largest pool, No. 16, was about 25 ft. long by 4 or 5 ft. wide, with a maximum depth of about 8 ins. The smallest, No. 36, held about half of a gallon of water. In the dry season, the flow was never rapid or strong and the stream afforded a natural trail up its rock-strewn bed through the heart of a dicotyledonous rain-forest typical of Panamanian woods (see Fig. 1).

Characteristic animals were collected singly and identified by various specialists, and certain drag-net collections were made with a dip-net in such a manner as to allow quantitative estimation of the larger inhabitants of the different pools. These collections brought out the following significant facts:

1. The moist stream bed is invaded by numerous land animals during the dry season, including such animals as termites and land lizards (*Ameiva festiva* Lich. e.g.).
2. Some animals were found in all the pools. These included *Pseudothelphusa richmondi* Rath., a crab, which was also found dead far above the last standing pool, indicating a wider distribution during the rainy season.

¹ The facts summarised in this note were gathered by the senior author while working at the Laboratory of the Institute for Tropical Research on Barro Colorado Island in Gatun Lake, C.Z., in January to March, 1924. The junior author assembled and calculated the crude data and made a preliminary draft of the manuscript. We are indebted to Mr James Zetek, resident custodian of the Institute, for local aid; to the Bache Fund of the National Academy for financial aid; to the specialists who identified parts of the collection who are listed in Allee, W. C. (*Ecology*, 7, 1926 a, see Bibliography) and to Marjorie Hill Allee for field assistance.

A frog, prominently marked with red on its posterior legs, *Rana warszewiczii* Schmidt, was found wherever there were permanent pools and another frog, *Eleutherodactylus rugulosa* Cope, was also generally present. A beetle, *Copelatus prolongatus* Sharp, and a hemipteron, *Ambrysus pulchellus* Mont., a near relative of *Belostoma*, complete the list of the animals that were generally distributed.

3. The majority of animals present showed some degree of differential distribution in the stream. Thus the lizard, *Basiliscus basiliscus* L., was limited to the lower region near Gatun Lake. The only fish present, *Brachyrophis episcopi* Steind., was not found above pool 17, but were common or abundant below that point. Pool 16 contained 84 of these fish, both small and large. Shrimps of several species were present: *Atya scabra* Leach, *A. occidentalis* Newport, *Ortmannia americana* Guerin, and *Macrobrachium jamaicense* Herbst, but were limited to the lower 24 pools.



FIG. 1. Pools 2 and 3 in Shannon Creek.

The water striders, *Rhagovelia insularis* Champ., *Velia brachialis* Stal., *V. cinctipes* Champ., *Limnogonus marginatus* Guer. and *Brachymetra albinervis* Am. and Serv., were mainly limited to the region below pool 25. No damselfly nymphs, dragon-fly nymphs or may-fly nymphs were taken above pool 16.

On the other hand, there were many more tadpoles in the upper pools, although they were to be found in all pools offering such shelter as is furnished by an accumulation of leaves on the bottom. They were so numerous in the upper pools that they fairly blackened the substratum. Tadpoles were found still within the egg-jelly in the upper pools about the 1st of March, but most of those present were over an inch long¹.

Water beetles, mainly *Copelatus prolongatus* Sharp, although found throughout, were definitely more numerous in the upper pools.

Table I gives the results of a series of similar dip-net collections of fish, shrimps and tadpoles in representative pools. The results have been calculated in terms of 100 litres and may be accepted as a close approximation to the truth.

Of the possible factors that might cause differential distribution in this stream we can eliminate temperature immediately, since the entire observed

¹ Dr Thos. Barbour, who was in Panama at the time, could identify these only as toad tadpoles. I have been unable to secure further identification.

Table I. *Numbers of fish, shrimps and tadpoles per 100 litres.*

Pool No.	Fish	Shrimps	Tadpoles
2	0.3	0.3	0.0
3	1.1	0.1	2.6
4	5.6	35.3	2.8
5	2.4	1.8	2.1
6	5.6	5.6	0.0
12	4.2	0.0	89.3
13	59.4	13.2	495.4
14	10.3	0.8	774.9
15	33.0	6.6	733.2
16	14.8	4.2	93.3

range for all the pools were only 24–25.1° C., as taken with a standard thermometer graduated to tenths of a degree. All the pools were usually shaded. None were seen completely exposed to the sun at any time during the day, but the upper ones were in general the more shaded.

With two exceptions, the dissolved oxygen of the first 24 pools was between 4 and 5 c.c. per litre (Winkler's method). Pool 5 showed 2.6 and pool 6, 10.3 c.c. per litre. The former was a compact, relatively deep pool with much bottom cover of leaves. The latter was a long, narrow, shallow pool with little cover over the rock, gravel and sand bottom. The fewer fish and shrimp in No. 5 may be correlated with the low oxygen content but the most significant difference in the life of the two was the marked scarcity of tadpoles in pool 6. Judging from their general stream distribution, this was due to a lack of bottom cover rather than to the high oxygen content of the water. Such a conclusion needs to be checked by exact experimentation.

The water trickling over the rocks showed an oxygen content as high as 12.34 c.c. per litre. The inlet of Gatun Lake into which Shannon Creek flows had 7.4 c.c. per litre in mid-afternoon. The oxygen content of the lake is kept high by the strong winds and by the large amount of green algae.

The *pH* of the water was determined by colorimetric methods with phenol-sulphonephthalein and dibromophenolsulphonene-phthalein as indicators, and with a set of recently prepared La Motte tubes as standards. The *pH* ran steadily at 7.5 in the first eight pools. From No. 9 to No. 23 there was a variation between 7.2 and 7.9 in the different pools. Pools 24 and 25 were found to be neutral (7.0), and the upper pools fell off to a characteristic *pH* of 6.6, but with a range of from 6.1 to 6.9 in various small holes containing water near pool 36. Water trickling over a rock near pool 36 was found to have a *pH* of 7.5; near Gatun Lake such water showed a *pH* of 8.0. The results of the temperature, *pH* and oxygen survey are given in Fig. 2.

The upper pools were distinctly acid. It will be remembered that the same pools had a low oxygen content. The pools much exposed to rocks or near water flowing over a rock bottom were more alkaline. The presence of many leaves made the water more acid, particularly if the leaves were much broken. The more rapid and direct the flow, the higher the *pH*. The reduced *pH* and

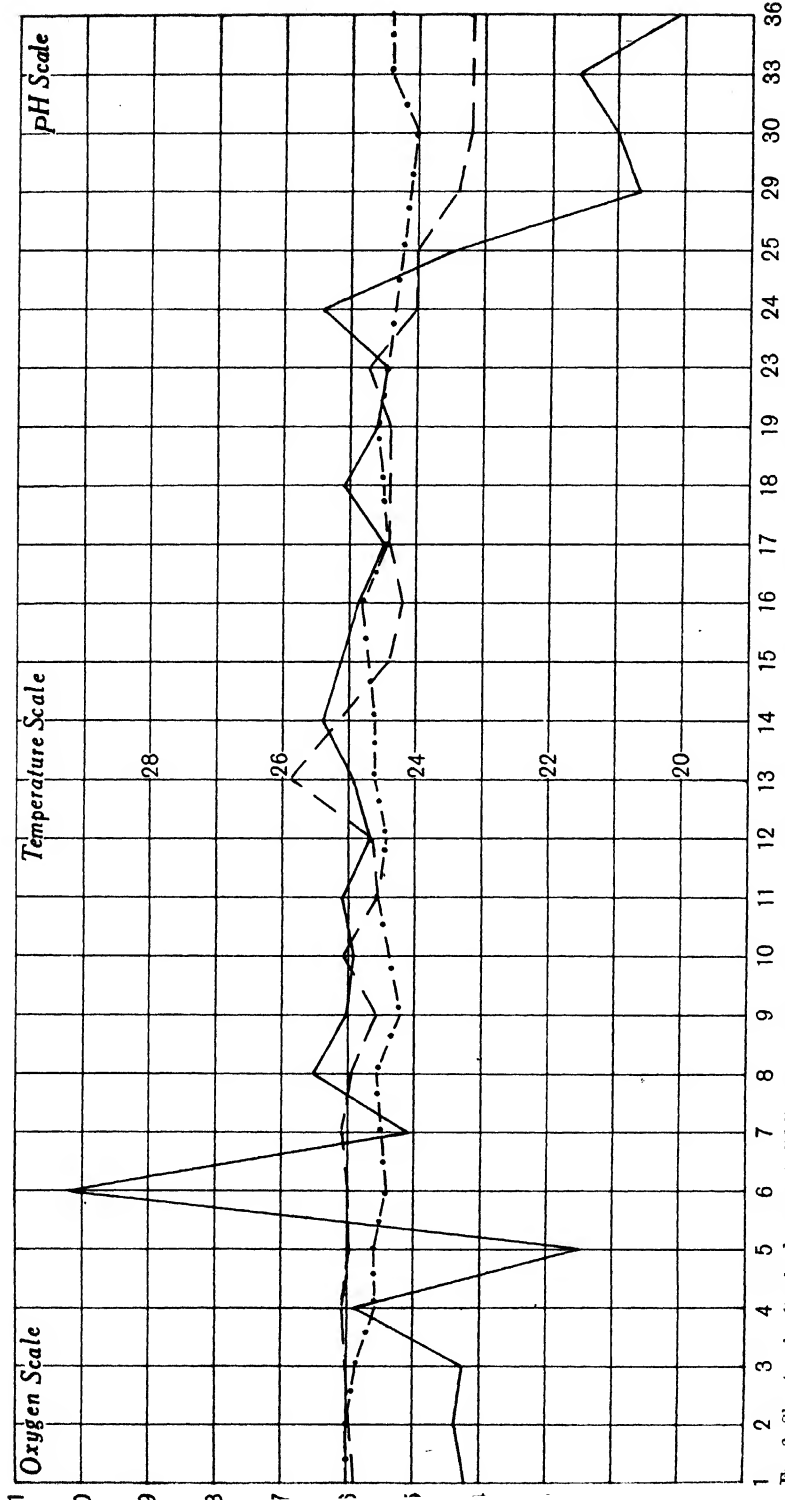


FIG. 2. Showing the dissolved oxygen (solid line), pH (broken line), and temperature (dotted line) of Shamon Creek pools. Numbers on the abscissae designate pools in their order from Gatun Lake. Those on the ordinates show oxygen in c.c. per litre, temperature in degrees Centigrade and pH.

70 *Animal Distribution in a Panama Rain Forest Stream*

oxygen tension in the upper pools is related in part to the lack of aeration after the ground water emerges.

In addition to the general decrease in pH in the upper stream there are some points of obvious interest in more localised sections. Pool 12 had a pH of 7.3, while No. 13, 20 ft. away and 8 ft. higher, showed 7.9. Both were about the same size, being 2 by 3 ft. on the surface and 4 to 6 ins. deep. There were no differences in the observed collections that could be attributed with any degree of certainty to the difference in pH . A variation of 7.3–7.9 was observed on different days in pool 10 without noticeable effect on the animals present. Gatun Lake ran a mean pH of 7.5 in the inlet near the opening of Shannon Creek.

The upper pools are decidedly smaller than the lower. The notes on size turn from estimated area to estimated gallons. Above No. 17 there was evidence of lack of permanence during the dry season, which was particularly marked above pool 25. Pool 36 seemed more permanent than many below and apparently was fed by a fairly constant sea of ground-water. The lack of permanence in the upper pools accounts for the lack of fish and shrimps there. The former disappear before there is a marked change in dissolved oxygen or in pH , and the latter are reduced in numbers before these factors change.

Except after the semi-occasional rains of the dry season, there is little more than ground flow above No. 18.

The largest number of animals was taken from the largest pool, although they were not in greatest concentration. A greater variety was taken in some of the smaller pools.

Pools having leaves on the bottom and a flow of water were more densely populated than those with a similar flow, but with little bottom covering. There were more animals present when the leaves were massed over rocks than when they were over sand or gravel. The marked difference in numbers of animals present in pools 12 and 13, which varied markedly in pH , can be easily explained on the basis of available cover.

When one views the differential distribution of animals in this stream in the light of the analysis of environmental factors, the observed differences in animal life, in oxygen tension, and in pH , all appear to be correlated with such conditions as size and permanence of pools, permanence of flow and amount of leaves present. In other words, the low oxygen tension and low pH are themselves determined by other physical conditions, some of which limit the distribution of animal life as well. Consequently, without direct proof, observed differences in oxygen and pH cannot be held to be a cause of the differential animal distribution in Shannon Creek¹.

¹ Conversely, it is worth noting that widely differing bodies of water have similar pH values. Thus Gatun Lake (7.5), Great Salt Lake (8.0, based on mid-lake value of 8.3 with corrections from McClendon and Medes, p. 117), Lake Michigan (7.9–8.4) and uncontaminated water from Woods Hole channel (8.0), to mention only those with which we are personally familiar, present a degree of similarity of pH which is not reflected in their animal life.

Doubtless both these factors can be and are limiting factors in the distribution of animals, yet the analysis of conditions in this tropical stream during the dry season, when differences are most marked, supports conclusions reached as a result of similar analysis of adlittoral animal distribution at Woods Hole, Mass., viz.: The distribution of animal associations normally depends on the entire environment and again emphasises the importance of the well-known factors of relative location and of character of substratum in the distribution of water animals.

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STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

V. THE WATER ECONOMY OF THE CHALK FLORA¹

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(With Folding Graph and twenty-nine Figures in the Text.)

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I. INTRODUCTION

THE dryness of the chalk has been one of its most widely recognised characteristics. The North Downs of Surrey and Kent afforded for many centuries a highway running east and west when the country on either side was too wet and too muddy to allow of easy transport. The ecologist has long recognised that the flora is of a xerophytic type and that the water supply is one of the chief determining factors of the environment, and yet we have little actual data on the subject.

This paper is a report of a preliminary investigation into the problems of the water relations of the chalk vegetation, carried out in the Botanical Laboratories of University College, London, under the direction of Dr E. J. Salisbury, and included in the present series of publications in order to bring together the available data for the English Chalk. As a starting point, it seemed essential to have some data as to the actual amount of water present in that part of the soil exploited by the roots, and also the range of variation in its distribution in time and space; and a record has therefore been made of the actual water content of the soil at successive depths from a chalk down

¹ Thesis approved for the Degree of Doctor of Philosophy in the University of London.

near Purley in Surrey. A site just below the actual crest, where the ground fell away slightly to the south-west, was selected for intensive study, since it gave good average results when compared with similar areas in the district; and a uniform series of samples was taken from it at four successive depths, ranging from the surface to 2 ft. 6 in. approximately, at weekly intervals over a period of some 18 months.

The area studied intensively, and to which all the figures in Table I refer, was some 10 yds. square: the successive borings for samples being taken at least 1 ft. distant from previous ones.

The surface soil was a brown friable loam (for analyses see Table IV); small lumps of chalk up to 0.5 in. (12 mm.) diameter occurred at a depth of 1 in. (2.5 cm.), and increased in size and frequency until the loam gave way to broken chalk at a depth of 8 in. (20 cm.). Solid chalk occurred at 10 in. (25 cm.). A few small flints were present, they were only rarely of sufficient size to prevent the auger being used at a given spot and chiefly occurred between 4 and 8 in. (10 and 20 cm.) below the surface. The pH values ranged from 7.4 at the surface to 7.6 for the underlying chalk.

The vegetation of the area included *Agrostis* sp., *Avena pubescens*, and *A. pratensis*, as the more abundant species, while intermixed with these were plants of *Bellis perennis*, *Briza media*, *Bromus erectus*, *Chlora perfoliata*, *Fragaria vesca*, *Galium verum*, *Gentiana amarella*, *Linum catharticum*, *Ophrys apifera*, *Poterium sanguisorba*, *Prunella vulgaris* and *Viola hirta*. The upper 3 in. of soil were abundantly occupied by roots, which were less frequent in the zone below, while in this area the lowest zone considered was tapped only by roots of *Galium* and *Poterium*.

The method employed was to remove the soil on the thread of a large auger, since it was found that in this way the soil from the lower levels could be removed without contamination from higher levels. The samples were immediately transferred to an air-tight box, weighed out in the course of a few hours and then dried at 100° C.

The values of the water content for samples taken quite close together may differ very appreciably—sometimes the variation amounting to as much as 3 per cent. at the surface levels for a couple of samples within 2 ft. of each other. Readings below the surface tend to be much more uniform, but it must be borne in mind that variations of this type occur at all the levels considered in the present survey; although, as in each case the figures given represent the mean value for a set of three samples taken approximately within a couple of feet, the effect of such variations is minimised.

The average value of the water content of the first 9 in. over the whole period was 31.7 per cent. (for the first 3 in. 36.8 per cent.), a value comparable to the mean value for the surface soil of the *Quercus robur* woods of Hertfordshire, 29.5 per cent. as recorded by Salisbury (1916), and to the maximum for the older sand dunes of Blakeney Point, 35.9 per cent. (Salisbury, 1922).

But it is the minimum values which will chiefly determine the character of the vegetation, and whereas the minimum values for surface water content for *Q. robur* and *Q. sessiliflora* woods recorded by Salisbury, 1916 and 1918, were 19 per cent. and 18.5 per cent. respectively, the minimum recorded for the top 2 in. of a chalk down was 8.58 per cent. It would therefore appear that the soil-water contents of the chalk down exhibit more marked fluctuations than those of a mesophytic community; and while high values may be attained, ranging in some instances to 98 per cent., it is the very low minimal values which determine to a great extent the character of the vegetation.

II. THE NATURAL WATER CONTENT OF CALCAREOUS SOILS

Table I. *Soil-Water Content of Given Site* (see p. 73).

	0-3 in. (0-7.5 cm.)	6-9 in. (15-22.5 cm.)	12-15 in. (30-37.5 cm.)	27-30 in. (68.5-76 cm.)
1924				
Jan. 12	40.8	25.0	22.8	22.8
14	30.63	23.30	21.65	22.40
20	29.45	26.50	28.36	23.79
27	26.58	25.70	24.68	26.02
Feb. 4	53.84	27.06	23.15	22.32
6	46.62	28.70	25.78	27.87
10	34.86	27.04	29.45	27.63
24	50.48	30.37	25.63	26.42
Mar. 2	41.05	28.13	20.55	20.35
9	39.47	30.54	26.74	27.06
16	35.67	25.78	24.84	27.87
22	30.72	34.93	25.78	26.68
23	51.97	32.73	27.40	27.81
25	38.21	31.60	29.10	32.12
30	45.79	29.52	26.26	32.28
Apr. 7	27.40	26.26	26.58	30.54
15	44.40	33.61	29.50	33.52
22	42.14	28.37	28.21	27.88
26	57.49	31.17	27.80	30.13
May 3	44.51	32.54	27.31	30.90
12	61.29	35.59	30.22	31.60
18	35.22	27.06	27.57	34.93
27	53.51	31.49	25.63	28.13
June 1	35.89	30.14	28.56	28.20
15	39.76	27.57	26.58	26.91
30	19.40	18.17	19.47	27.22
July 13	12.48	12.29	22.32	23.68
21	39.37	20.55	20.12	21.19
Aug. 4	40.15	28.47	26.42	26.74
20	39.86	24.68	27.00	24.68
31	37.81	28.36	29.61	28.30
Sept. 28	42.45	28.13	28.53	27.81
Oct. 5	41.84	31.78	30.37	31.69
12	43.98	29.95	32.72	31.60
19	40.80	26.50	31.26	29.82
26	41.37	27.93	30.10	29.56
Nov. 2	38.12	33.71	30.04	29.28
10	29.53	27.80	29.96	27.24
15	51.51	29.89	27.64	32.19
23	39.37	32.28	30.54	27.97
30	42.41	31.32	31.52	30.04
Dec. 7	42.45	29.20	29.70	29.54
20	42.59	31.02	30.96	30.67

Table I (*continued*).

1925		0-3 in. (0-7.5 cm.)	6-9 in. (15-22.5 cm.)	12-15 in. (30-37.5 cm.)	27-30 in. (68.5-76 cm.)
Jan.	1	42.07	30.37	30.72	34.32
	11	43.10	30.74	29.88	30.01
	18	47.20	30.26	30.54	30.74
Feb.	1	54.56	27.97	31.66	31.49
	15	58.76	33.42	34.05	31.56
Mar.	1	54.44	33.16	26.58	27.00
	8	38.80	30.80	29.61	27.06
	22	44.09	28.86	31.23	28.95
	5	37.74	27.00	26.50	26.59
Apr.	19	39.47	26.91	28.94	31.32
	26	41.37	30.54	28.05	30.07
	3	40.15	32.80	27.65	31.15
May	17	31.60	24.48	27.00	25.14
	3	18.84	21.24	24.93	24.24
June	7	16.26	20.05	23.18	27.57
	12	15.89	16.60	21.66	22.32
	17	13.50	14.63	17.91	19.89
	28	10.19	14.74	16.96	17.78
	6	8.58	11.50	12.37	15.94
	7	17.79	12.12	10.76	15.72
	13	8.80	12.65	13.88	15.34
July	19	8.89	11.72	—	—
	8	29.52	22.32	23.15	23.10
Aug.					
Mean 1924-5		36.78	26.63	25.84	27.20
Maximum		61.29	35.59	34.05	34.93
Minimum		8.58	11.50	10.76	15.34
Total range of variation		52.71	24.09	23.29	19.59

(a) SEASONAL DISTRIBUTION OF WATER.

On the site selected for intensive consideration, samples were always taken at depths of 0-3 in. (0-7.5 cm.), 6-9 in. (15-22.5 cm.), 12-15 in. (30-37.5 cm.) and 27-30 in. (68.5-76 cm.)—and frequently at intermediate levels as well.

The records were taken at short intervals from January 1st, 1924, to August 1925, thus covering a variety of weather, beginning with average open winter conditions, then a long dry and frosty spell, constituting a spring drought, a wet May and early June followed by a short dry spell which was the climax of 1924. Subsequent weather was dull and wet so that in most parts of the country there were floods from December 1924 to the end of February 1925, and even the soil at the surface of the chalk down under consideration some 400 ft. above sea level was super-saturated for a period of about 7 weeks. A comparatively dry spring followed, giving place to a long and critical period of drought lasting throughout June and the greater part of July. By the end of the first week in August 1925 there was not any apparent vestige of the drought effects so far as the actual water content of the soil to a depth of 30 in. was concerned.

The rainfall, being the chief source of water supply, determines to a large extent the variation of the soil-water content in time, although those factors controlling the evaporation from the surface are also of primary importance. Church (1922) has stated that the hours of rainfall are probably of more

significance than the actual amount, thus implying the importance attaching to the humidity of the atmosphere, and the present records certainly show that evaporation is a vital factor influencing the variability of the water content of the surface layers of soil.

Through the kindness of Mr J. E. Clarke I have had access to the daily rainfall records for the ridge of down next to that from which the present data were taken; this station is rather less than a mile away and the two are in positions closely comparable as regards height above sea level, aspect and angle of slope. The daily evaporation data have been taken from the nearest station at which such records were made (i.e. Addington), and for access to these records I am indebted to Mr G. F. Carter. Addington is 5 miles away; and while it would be much more satisfactory if the records were obtainable from a nearer place, it was felt that the general weather conditions were sufficiently similar to supply data from which some conclusions might be drawn. (At Addington the evaporation is measured by the fall in level of a free water surface.)

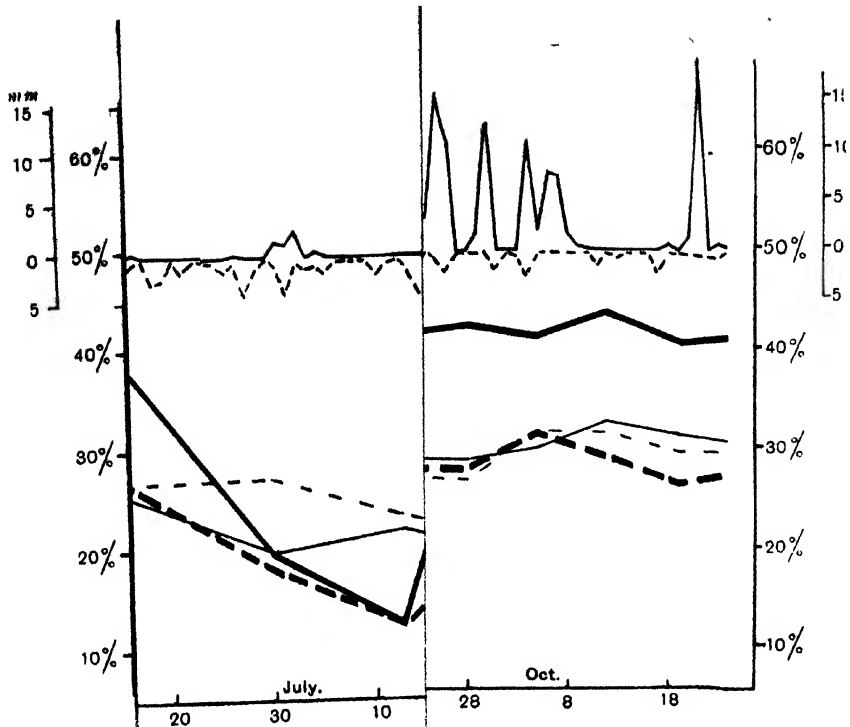
In the accompanying diagram (Fig. 1) the rainfall curve for Purley has been shown together with that for evaporation as based on the Addington records. It is thus possible to deduce approximately the water available for percolation through the soil. This would not be true for many soils, but the porosity of the chalk is an important factor and generally speaking very little water is lost by surface drainage.

It must be noted that the exceptionally dry character of the early summer of 1925, and the wet season of 1924 render it probable that these data represent the range of fluctuation for this type of habitat more nearly than might be anticipated from a much longer period of observation.

At the outset the curves (Fig. 1) show the importance of evaporation as a factor influencing the soil-water content. Thus January 1924 was a wetter month, i.e. had a greater total rainfall, than February, and yet the surface of the ground is wetter in February: this may be accounted for by the fact that the latter was a dull foggy month with evaporation only two-thirds of that recorded for January.

During February and March 1924 deposition of moisture was mostly in the form of snow, and this remained on the ground for considerable periods. The long spell of 41 consecutive ground frosts came to an end on March 22nd, by which time the surface soil had become relatively dry, having lost moisture steadily during the latter part of this cold period, as a result of the cold and dry east winds which were then prevalent.

By contrast April and May gave high water contents obviously to be correlated with the heavy rainfall. A point which is particularly noteworthy in the April record is the abnormally low water content at the surface recorded for April 7th (27.40 %), which would not seem to be satisfactorily explained by the previous 10 days' spell of fine weather, although the evaporation during



Above these are shown the rainf

this period was doubtless an important factor. The effect of this "drying" period is also seen at the 6-9 in. level.

There follows a very wet spell when the surface soil was super-saturated for rather less than a month. If the curve for this period is compared with that for the other wet period, February 1925, the irregularity of the May curve is very apparent. The low values obtaining on April 22nd, May 3rd and 18th, were each preceded by spells when the recorded evaporation was more than counterbalanced by the rainfall, and it is obvious that they may be directly attributed to this. By contrast the February 1925 evaporation was negligible and the surface-water content is steadily maintained at a high level throughout the wet period.

In both 1924 and 1925 there is a marked decline in water content, particularly at the surface with the onset of the period of greatest vegetative activity in the flora. In 1924 this is very noticeable at the end of May and first week of June, and seeing that this was a period of high rainfall and that the ground was already super-saturated, the sudden fall can scarcely be attributed to the weather conditions, and indeed is the opposite of what might be expected. In 1925, which was a rather earlier season, all levels show a steady fall early in May before the drought set in.

The dry spell in July 1924 was too short to be of much importance but the 1925 drought was the most significant period which came under observation. No rain fell from May 29th till June 24th, and although there was a slight fall then and another on July 6th, it was not until July 18th that the weather really broke.

The period constitutes a rather more severe drought than is usual in this country, although scarcely comparable to the exceptional drought of 1921, and since it became established early in the year, in a season normally of rapid growth, it may be regarded, from an ecological point of view, as of more significance than a longer drought occurring when most of the herbaceous plants are drying up and ripening their seeds.

During this time there were fairly heavy dews and an attempt was made to see how far they could directly influence the soil-water content. In dealing with the usual surface samples of 0-3 in. the dew effect was imperceptible, but there was an appreciable difference in the first inch when this was tested alone. Thus an average of 12 samples of the top inch (2.5 cm.) of soil taken at 4.30 a.m. (June 17th), before the sun reached the down, gave a water content of 8.8 per cent.; the corresponding value taken at 5 p.m. on the previous afternoon was 8.2 per cent., which agreed closely with the average readings for noon on the second day, 8.16 per cent. Apart from the significance which deposition of dew has in depressing the rate of transpiration, its effect upon the water content of the top inch of soil is no doubt important in connection with the surface roots found in many of the grasses present as well as those of such plants as *Chlora* and *Thymus* (see below, pp. 92, 109).

During the later summer period, July to September, when part of the flora is dormant (see pp. 119 *et seq.*), the average surface-water content is 24·8 per cent. and at 6–9 in. 19·3 per cent., but for June and July alone it is 16·6 per cent. and 19·1 per cent. respectively. During the winter months, November to January, the corresponding mean values are 41·0 per cent. and 30·7 per cent. It must be noted that the range of fluctuation between winter and summer values at a depth of 6–9 in. is very much less than at the surface, a fact of considerable importance in relation to the depth of penetration of root systems (see p. 90).

Once the summer had passed its climax the water contents during the decline of the year tended to be less variable, as was also the weather. It is noteworthy that a spell of fine frosty weather, such as that occurring in November 1924, is at once effective in reducing the surface-water content.

(b) VERTICAL DISTRIBUTION OF WATER.

As has already been mentioned, the soil samples from the site selected for intensive consideration were always taken at depths of 0–3 in. (0–7·5 cm.), 6–9 in. (15–22·5 cm.), 12–15 in. (30–37·5 cm.) and 27–30 in. (68·5–76 cm.); they were frequently taken at intermediate levels as well.

During periods of drought the water content was found to increase with increasing depth, this being the more marked the longer the continuation of the dry spell. But for the greater part of the year, especially during and immediately after rainy periods, the soil was wettest at the surface, the water content decreasing with increasing depth. Frequently, however, it was found that the driest zone examined was at 12–15 in. and that there was a subsequent rise of water content in the foot or so below. This was hardly to be expected, and consideration of this point must be deferred (see p. 80).

Considering the top 3 in. of soil, it was found that the mean water-content value for the whole period was 36·8 per cent. and the range of variation 52 per cent. (see Fig. 2). At saturation the water content was 45·5 per cent. and the records show that the surface layer was super-saturated on seven separate occasions during 1924 and for a period of over 6 weeks during January and February 1925.

The maximum recorded for the surface was 61 per cent. on May 12th, 1924, after a long wet spell which similarly influenced the 6–9 in. level, as the maxima recorded for the two levels occurred on the same day.

Values considerably over 61 per cent. were recorded for the surface of Farthing Down, another chalk area some 2 miles distant, where a close turf extends over a treeless down for several square miles, but where the top soil to a depth of 7 in. or more consists of a thoroughly leached layer of dark loamy soil, destitute of CaCO_3 , sharply delimited by a compact layer of large flints from the chalk below. Here values up to 98·4 per cent. of water at the surface were recorded, but this appears to be exceptional.

The lowest value obtained for the water content of the surface was 8.58 per cent. This was recorded on July 6th, 1925, after almost 6 weeks of drought. A slight rainfall caused a sharp rise in the surface-water content next day but in less than a week the effect of this was scarcely perceptible, and although the drought lasted another week the surface did not become any drier. Although the evidence available is insufficient to form the basis of any conclusion, it is possible that some kind of equilibrium between loss by evaporation and gain by capillary supply from below may have been established at this value. For 7 weeks the upper 3 in. of the soil had been the driest part, and, as will be shown later, there are a number of plants, including the bulk of the grasses, which are chiefly dependent on this zone for their water supply, yet none of these appeared to be seriously affected.

It would appear from the literature that this minimum water content for the top 3 in. of soil, i.e. 8.58 per cent., is much lower than is usual in mesophytic communities; and experiment showed that only some 3-4 per cent. of this was available to the plants (see p. 123 *et seq.*), while under certain conditions a water content of over 10 per cent. was found to be insufficient to support the life of certain species. It must be pointed out that where minimal values lower than 8.58 per cent. are recorded, as for the Cottonwood Dune Association (Fuller, 1912) with a minimum of 2 per cent., and as also occurs on the young dunes at Blakeney, the surface is unscreened by a continuous carpet of vegetation.

Below the surface 3 in. the water conditions at subsequent levels examined were much less variable, chiefly because they are influenced to a very much smaller degree by evaporation, and there appears to be a definite correlation between the curves obtained for the several zones.

At a depth of 6-9 in. the range of variation in the water-content values was 24 per cent. or rather less than half that experienced at the surface; though approximately the same as at 12-15 in.

The lag between precipitation and rise in water content, which is so conspicuous a feature of the deeper chalk, where it amounts roughly to 3 months, is of comparatively little importance in the region exploited by the roots of herbaceous plants. Between the surface and the 6-9 in. level the lag amounts, on the average, to rather less than a day. It will be noticed that the maxima recorded for the two levels coincide, occurring on May 12th, 1924; and during dry spells, as in July 1925, a heavy fall of rain will make an increase in the water content at 6-9 in. within 24 hours.

During this dry spell in 1925 some watering experiments were carried out, and the results obtained give a rough indication of the normal lag in a dry chalky soil. When a gallon of water was evenly distributed over a square yard of ground the lag was found to be between 18 and 20 hours at 6-9 in. depth.

Except during the summer drought of 1925, there was only one occasion upon which the water content at 6-9 in. was greater than that for the surface.

This was on March 22nd, 1924, at the end of a long spell of dry frosty weather, to which reference has already been made; but it is worth remarking here the similarity of effect between spring and summer droughts.

A consideration of the lower levels, i.e. 12–15 in. and 27–30 in., shows the range of fluctuation in the water content to be only slightly less than that for 6–9 in. (see Fig. 2, also Table I).

The lag between the rainfall and the water-content values at 12–15 in. may vary between 2 and 4 days, and it is probable that this variability may be accounted for by the difference in depth at which the fairly loose chalk gives

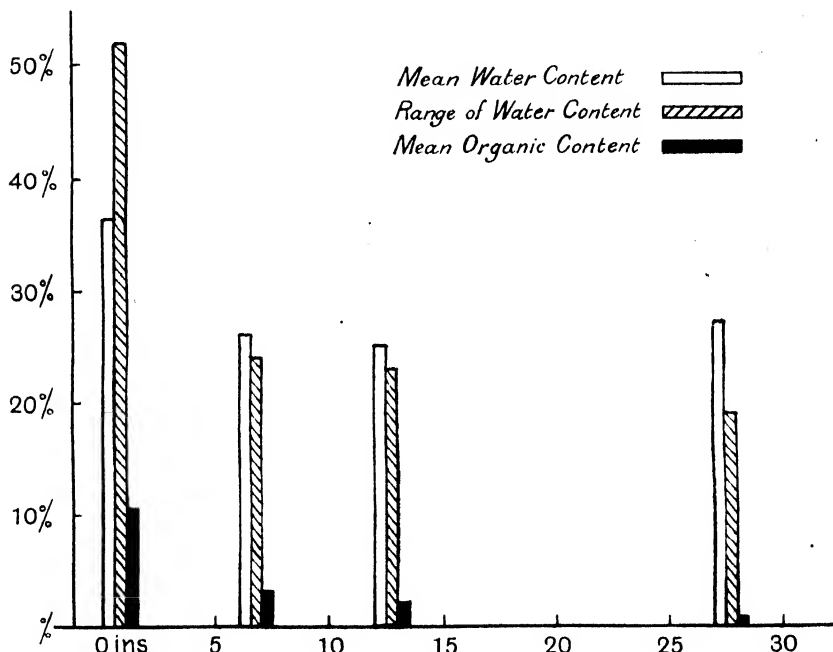


FIG. 2. Composite diagram showing the mean water content at four different soil depths over a period of eighteen months, and also the range of variation experienced at these levels during the same period. The organic content at the different levels is also shown.

place to the underlying solid rock and the nature of this transition zone. The rate of percolation depends on other factors than soil texture and the amount of moisture present in the soil may be of more importance.

At a depth of 27–30 in. the lag experienced may vary between 5 and 8 days, but such general trends at this level would seem to be frequently masked by other movements of water in the soil.

Taking the mean water content for the whole period, it is found that the 12–15 in. level tends to be the driest, and in the light of certain other observations this seems to be significant. Thus, if the records for 1924 alone are considered, it is found that the zone which showed the least variation was the

12-15 in. level—a quite unexpected result. Further, it will be noticed that there is sometimes a marked rise in the water content at 27-30 in. which it seems difficult to attribute to percolation (e.g. January 1st, 1925, or June 7th, 1925). It therefore seems probable that some factor is operating on the water content at 27-30 in. more actively than on the levels above.

Isolating part of the curves for the two lower levels, it will be noticed that a rise of water content in the lowest zone may frequently be followed some days later by a rise in the 12-15 in. level, e.g. November 15th, 1924. This may be interpreted as indicating an upward movement of water in the soil, by capillarity. It therefore seems that some of the high values obtained for the 27-30 in. level are due not only to the water present as a result of percolation, but also to a supply of water travelling upwards from the region of the permanent water table by capillarity.

This upward movement of water would also explain the steady absolute rise recorded at 27-30 in. throughout March 1924, which was a period of spring drought, this rise being present, but less marked in the 12-15 in. zone, and just appreciable at 6-9 in.

Many years ago Ansted showed that under experimental conditions water will rise in chalk by capillary action for a distance of 16 ft., and it would seem that this force is of considerable importance in natural chalk soils.

(c) EFFECT OF SLOPE AND VEGETATIVE COVERING ON WATER CONTENT.

Table II. *Water Contents of Crest and Slope.*

(Percentages of water.)

		0-3 in. (0-7.5 cm.)	6-9 in. (15-22.5 cm.)	12-15 in. (30-37.5 cm.)	27-30 in. (68.5-76 cm.)
Mar. 9	Crest	36.33	27.63	25.63	27.06
	Slope	35.49	27.22	24.60	20.49
Mar. 9	Crest	39.47	30.54	26.74	27.07
	Slope	33.33	25.63	23.79	25.39
Mar. 25	Crest	38.21	31.60	29.10	32.12
	Slope	45.45	24.68	23.15	24.08
May 12	Crest	61.29	35.59	30.22	31.60
	Slope	44.30	35.32	26.58	26.18
May 18	Crest	35.22	27.06	27.57	34.93
	Slope	43.47	25.94	27.00	26.26
July 21	Crest	39.37	20.55	20.12	21.19
	Slope	34.76	17.16	15.74	17.55

One fact which has appeared quite clearly during the investigation is shown in Table II—that the steeper slopes of the down tend to have a lower water content than the crest. (Readings were taken half-way between the top of the down and the valley floor, where the slope had an angle of some 23°.)

It is naturally to be expected that the surface layers of the slope would lose the water falling upon them more rapidly than the comparatively dry crest owing to surface drainage and that this would indirectly influence the

water content below the surface. But, owing to its porosity, there is far less surface drainage on the chalk than on most soils, and, to a certain extent, the central part of the slope, which is the part here under consideration, would, if surface drainage were important, tend to receive more water from the higher levels than had originally fallen upon its surface. Again, the increased exposure at the crest favours evaporation and would tend to keep the soil there dry. It is, therefore, somewhat unexpected to find that on the average not only is the water content at the surface rather greater at the crest than on the slope, but that there is a very definite tendency for this difference to increase with depth (see Fig. 3), so that at 27-30 in. the soil on the slope is usually con-

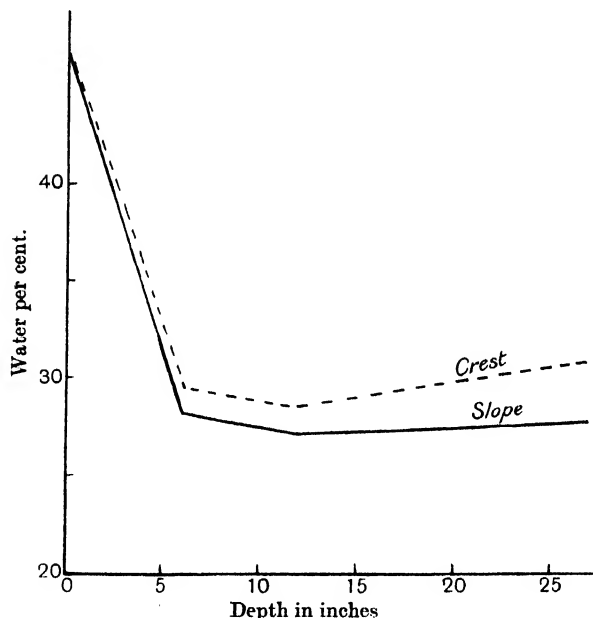


FIG. 3. Composite diagram showing the average percentage water content on the crest and slope of the down based on six series of records.

siderably drier than at the crest. At this depth the chemical composition of the soil is approximately equivalent for the two stations, giving over 90 per cent. calcium carbonate.

That the dryness of the slopes in comparison to the crest was not merely a local phenomenon was shown by the agreement of similar records from the Chilterns near Tring and from other areas; and, moreover, since such general tendencies were found to be true of slopes with S.W., N.W. and N.E. aspects, it is obvious that they were not due to differences in insolation or precipitation per unit area.

The factor which usually shows the closest correlation to the water content variations in calcareous soils is the organic content, and the accompanying Table III shows the average organic content of the soil on crest and slope,

together with the average water contents of several series taken at corresponding times for the two positions.

Table III. *Average Organic and Water Contents.*

	Crest		Slope	
	Organic	Water	Organic	Water
0-3 in.	10.75	46.98	9.09	46.94
6-9 in.	3.06	29.54	3.16	28.29
12-15 in.	1.18	28.67	0.80	27.42
27-30 in.	0.45	30.86	0.62	27.63

But these data show a lack of correlation between the water contents and the organic contents. This is most striking at the lowest level, which, being the zone least subject to leaching, makes it clear that the "clay" fraction (see p. 84) is not the disturbing factor, and this is further borne out by the fact that the surface layer exhibits the closest correspondence. The discrepancy being greatest at the lowest level, the probability is that the difference in water content between crest and slope is dependent on differences in capillary water supply.

It was found that when the covering of vegetation was removed, together with the top inch of soil, there was a marked decrease in water content—and not only is the bare chalky soil more dry at the surface, but the difference is even more strongly pronounced for the deeper levels. The portion of soil removed with the vegetation was of course the layer with the highest organic content and this may have been as important a factor in influencing the water content as was the grassy covering itself; but apart from this the higher temperature (Kraus, 1911) would have favoured evaporation from the bare chalky surface.

Table IV. *Water Content of Bare and Grass-Covered Surfaces.*

		0-3 in. (0-7.5 cm.)	9-12 in. (22.5-30 cm.)	24-27 in. (61-68.5 cm.)
Dec. 10	Bare	19.26	19.40	12.04
	Grass	26.26	24.21	19.40
Dec. 16	Bare	25.03	21.36	18.35
	Grass	26.74	25.16	24.84

NOTE.—In each instance the readings forming pairs were taken within 6 ft. of each other.

(d) RELATION OF WATER CONTENT TO CaCO_3 , "CLAY" AND ORGANIC MATERIAL.

Reference has previously been made (p. 73) to the variations in water content which may occur in samples taken but a foot or two away from each other, and in this connection an attempt has been made to throw light on the relations between the water and some of the other soil constituents.

Samples were collected in the usual way, and after drying at 100°C . the total carbonates present were ascertained by means of a calcimeter. In order to determine the humus, and the residual inorganic content, a weighed

quantity of the dry soil was ignited so as to leave only inorganic ash, but it was found that this method was unsatisfactory, since the carbon dioxide was only driven off from the carbonates with great difficulty. The following method was therefore adopted: 5 gm. of oven-dried soil were treated with 5 per cent. HCl until all the carbonates had been acted upon, the sample being then filtered through an ashless filter paper and dried. The loss on ignition is taken as the organic content and the residue as representing approximately the "clay" fraction.

When the results are plotted it is found that the curve for water content, while not following closely the curve for any one of the soil fractions, bears a more definite relationship to the organic content curve than to any other. This is particularly well shown for November 9th, 1924 (Fig. 4), where the remarkable rise in water content at 12-15 in. is to be correlated with a heavy rainfall 8 days previously, percolation having presumably been rather slower than usual owing to the somewhat high organic content. Considering the two sets of curves for December 7th, 1924 (Fig. 5), the correlation between water and organic content is again seen and is particularly convincing for the slope. Bearing in mind that the daily fluctuations in rainfall, percolation and evaporation have a continuous influence on the water-content curve, it is all the more remarkable that the relationship between the two appears so clearly. It must be noted that the highest water contents obtained for any open chalk down in the district always come from Farthing Down, the black loamy surface layer of which has an organic content of 26.9 per cent., or nearly three times that at the surface of the area under intensive examination.

These points, considered in conjunction with the previous evidence with regard to water variations on crest and slope, and on bare soil and that with a grassy covering, all tend to emphasise the importance of the organic content in influencing the water content (see Fig. 6, p. 87).

The accompanying Table V (p. 86) shows the soil analyses and water contents for a number of series together with the average values obtaining at the different depths.

Presumably the water in a given sample of chalk soil is roughly equivalent to that held by the calcium carbonate, together with the "clay" fraction and the organic material respectively. If we may assume that at the saturation point the water present is held by each factor to its utmost capacity, we can equate the CaCO_3 together with the "clay" and organic fractions to the water content, and by a series of such equations, deduce approximately the values as to the water-holding capacity of the respective soil fractions. The relative values thus evolved were:

CaCO_3	0.2
"Clay"	0.6
Organic	1.75

It was found possible to check the first by finding the water-holding

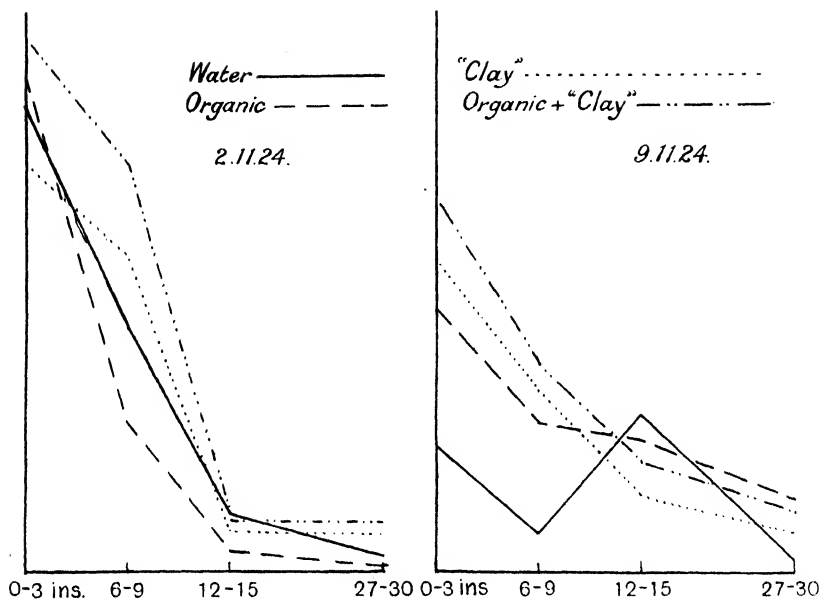


FIG. 4. Examples of graphs illustrating variation of water content and other soil factors with depth.

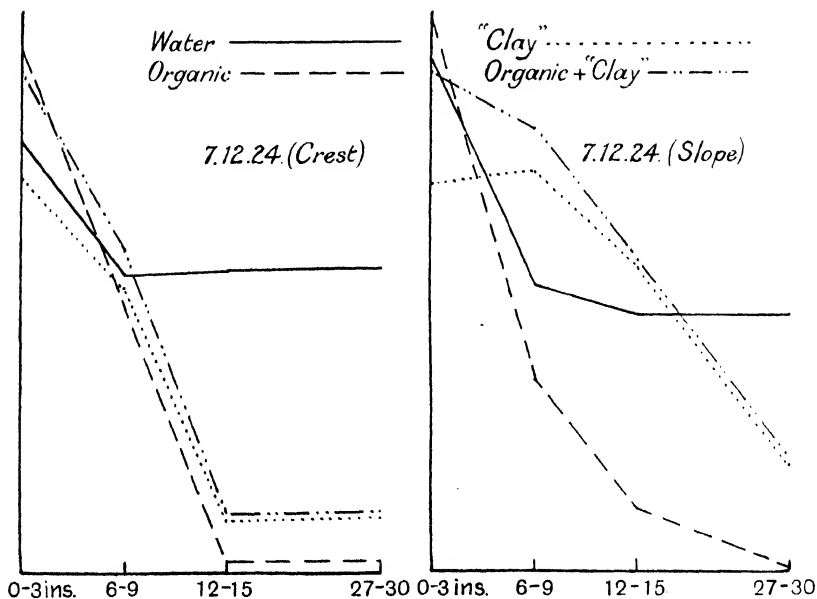


FIG. 5. Two examples of graphs showing the respective soil constituents for crest and slope in relation to the water content.

capacity for a block of pure chalk, this was 20·02 per cent. or approximately 0·2 of the dry weight, a value which is thus seen to agree closely with the value deduced on theoretical grounds. The values for all these soil fractions were found to be roughly correct for the various series obtained, whether for crest or slope of the down, and it may therefore be considered that the organic

Table V. *Soil Analyses.*
(Percentage values.)

	Depth (in.)	Water	Total car- bonates (chiefly CaCO ₃) <i>x</i>	Clay and sand <i>y</i>	Organic <i>z</i>
Nov. 2	0-3	38·12	58·21	32·07	9·72
	6-9	33·71	72·26	24·87	2·85
	12-15	30·04	96·65	2·91	0·43
	27-30	29·28	97·18	2·77	0·05
Nov. 9	0-3	29·53	70·37	24·23	3·40
	6-9	27·80	80·06	14·13	2·81
	12-15	29·96	91·36	6·01	2·74
	27-30	27·24	95·77	2·89	1·34
Nov. 16 Crest	0-3	51·51	48·15	37·41	14·44
	6-9	29·89	70·40	26·60	3·60
	12-15	27·64	91·20	6·40	2·40
	27-30	32·19	95·90	3·76	0·34
Nov. 16 Slope	0-3	43·57	66·07	26·64	7·29
	6-9	28·54	73·55	23·41	2·83
	12-15	29·45	85·06	14·00	0·94
	27-30	29·72	91·86	6·88	1·26
Nov. 23	0-3	39·37	53·66	34·12	12·22
	6-9	32·28	75·20	21·84	2·96
	12-15	30·54	93·80	4·94	1·26
	27-30	27·97	96·65	2·64	0·76
Nov. 30	0-3	42·41	53·06	32·40	14·54
	6-9	31·32	80·86	17·14	2·00
	12-15	31·52	93·60	6·56	0·00
	27-30	30·04	96·61	3·88	0·00
Dec. 7 Crest	0-3	42·45	50·92	38·34	10·24
	6-9	29·20	68·96	26·88	4·16
	12-15	29·70	94·86	4·90	0·24
	27-30	29·54	94·66	5·08	0·26
Dec. 7 Slope	0-3	50·37	50·96	38·14	10·90
	6-9	28·05	56·94	39·36	3·70
	12-15	25·39	69·60	29·74	0·66
	27-30	25·54	89·86	10·54	0·00
Averages Crest	0-3	36·78	54·99	33·17	10·75
	6-9	26·63	74·62	21·81	3·06
	12-15	25·84	93·58	5·29	1·18
	27-30	27·20	96·13	3·51	0·45

fraction tends to hold nearly nine times, and the "clay" fraction three times, as much water as the chalk itself.

The impure clay fraction as defined above in the typical chalk-down soils examined may be nearly 39 per cent. at the surface or as low as 24 per cent., whilst in all the samples examined there is a continuous decrease in the clayey residue as we descend, and at a depth of 27-30 in. this ranges from 2·6 per cent.

to 5.1 per cent. (or 10.5 per cent. on the slope). Such a definite gradient shows that the high values for the non-calcareous fractions at the surface are the result of leaching and are not the outcome of transport of material.

Where clay pockets occur in the chalk, they are found to be generally moister than the surrounding chalk, this being in agreement with the greater water-holding power of the "clay" fraction as shown above.

The following example shows the order of difference which may occur, the two sets of readings being taken from points 4 ft. apart:

17. ii. 1924	0-3 in.	6-9 in.	12-15 in.	27-30 in.
Clay pocket	50.6	45.7	40.2	38.6
Chalk	51.3	36.1	30.4	27.3

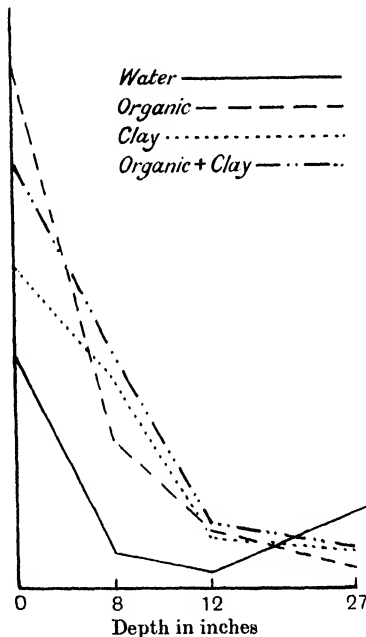


FIG. 6. A composite diagram showing the average of nine series of soil analyses. It will be observed that the water curve approximates more closely to the organic, than to any other shown.

(e) SOIL AERATION.

An attempt has been made to find the proportion of air in the chalk soil by using alcohol to displace the air from a block of undisturbed soil of known volume.

A cylindrical steel borer was used at first to obtain samples of earth, but it was found that although this cut a neat block and extracted it efficiently from the soil, it could not be removed from the instrument without undue compression or disorganisation. It was found that the most satisfactory method was to cut out blocks of soil with a knife and in this way several series were obtained.

Where the surface-water content had an average value of 44 per cent. a series of seven samples from the same horizon gave an average air content of 26.1 per cent. by volume.

For a rather higher water content (viz. 58 per cent.), the air content was, as would be expected, slightly less, viz. 24.5 per cent.

The method is perhaps most useful in affording a basis for comparison of the air content of the soil at various depths, and the results of five series of readings taken from the area of down intensively studied may be summarised thus:

Depth (in.)	Average air content %
0-1	25.9
1-2	21.5
3-4	12.2

The surface soil here had an average CaCO_3 content of 55 per cent.; while for a slightly more leached, though otherwise comparable area on the same range of downs and with a CaCO_3 content of 38 per cent., the corresponding values obtained were as follows:

Depth (in.)	Average air content %
0-1	11.9
1-2	10.5
3-4	9.6

All the above values refer to the open grass-covered down, and they may be compared with the results obtained for the surface soil of an oak-hazel coppice on clay with flints overlying the chalk, and situated on the opposite slope of the valley. Here an average of six readings gave 10.4 per cent. air content for the surface clay in the wood and on the same day 24.5 per cent. for the surface of the open down.

It is therefore apparent that the calcareous soil of a chalk down is well aerated and thus favourable to the development of deep root systems.

III. THE ROOT SYSTEMS OF CHALK PLANTS

The study of the distribution of water in the soil is a necessary preliminary to the study of the water problems of the plants themselves, foremost in which an attempt has been made to study the root distribution of rather more than fifty species of the chalk down flora.

Considering first the depth of penetration, there was found to be a well-marked range of variation amongst the herbaceous plants of these calcareous grass lands. As has been pointed out by Tansley and Adamson (1925), there is nothing comparable here to the conditions obtaining in American grass lands as described for the prairies of Nebraska by Weaver (1919, 1920), where only 14 per cent. of the perennials described have root systems less than $3\frac{1}{2}$ ft. deep.

On our own chalk downs the upper 3 in. of soil are very fully occupied by the roots of the dominant grasses, and while the roots of such plants as *Convolvulus arvensis* and *Centaurea scabiosa*, which are not typical members of the chalk grass-land community, were found to penetrate into the solid chalk rock to a depth of more than 4 ft., some of the characteristic plants may have roots 2½ ft. deep but seldom more.

For practical purposes three classes of root systems have been recognised, the divisions, being purely arbitrary, are as follows:

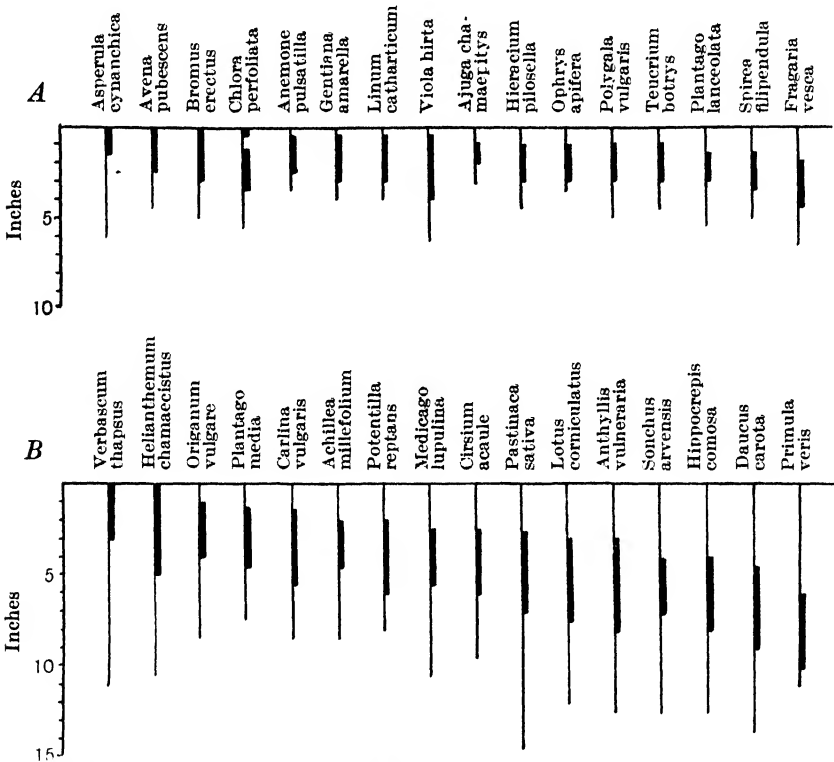


FIG. 7. Diagram of the rooting depths of certain chalk plants; the thick line shows the average zone at which the maximum development of feeding roots occur, while the thinner line shows the maximum depth of penetration attained. Above, plants of Group A. Below, plants of Group B.

- Plants with roots usually confined to top 6 in. of soil (Fig. 7 A).
- Plants with roots to depth of more than 6 in. and up to 15 in. (Fig. 7 B).
- Plants with roots to depth of more than 15 in. (Fig. 8).

Descriptions of the root systems of some of the more characteristic species of the chalk down follow: except where mentioned, the descriptions refer to specimens from the same stretch of down as that to which the bulk of the water-content data refer, or to neighbouring areas of strictly comparable structure. The figures given for the average working depth indicate the zone

at which the chief feeding roots occur. It was found that the mean of the average working depths for some 50 typical species was 4–8 in., while their mean maximum penetration was 12.1 in.

It is significant that among these plants the maximum number of feeding roots occur at a level in the soil at which we can assume the most happy combination of factors to obtain. Thus, as we descend, the air space in the soil diminishes, although the gradient is not so marked as in woodland soils (E. J. Salisbury, 1925). Consideration of the minimum water content ex-

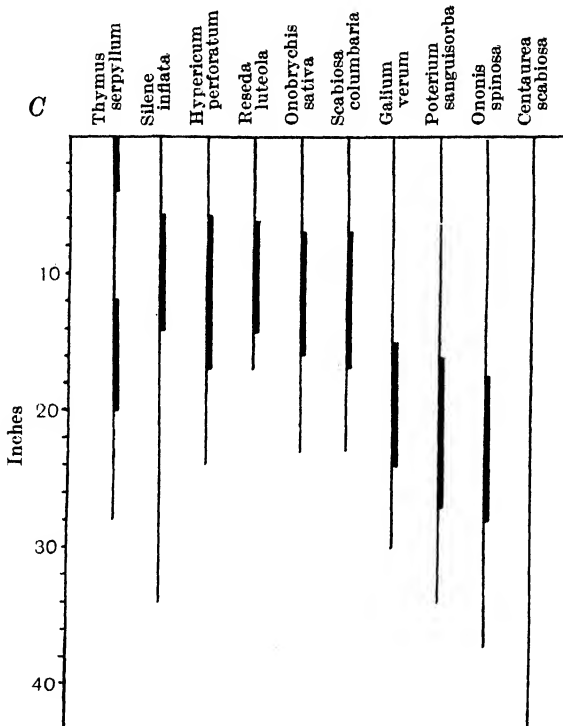


FIG. 8. Diagram of the rooting depths of Group C. Notation as in Fig. 7.

perienced at the various levels examined (see Table I) show that the 6–9 in. zone tends to be less dry than the zones either above or below, and it is these minimal values which are of prime importance. Again, while the range of fluctuation of water content is much greater at the surface, it shows no significant diminution between the 6–9 in. zone and that at 12–15 in. It is therefore at a short distance below the surface that the optimum combination between factors of water content and aeration probably occurs.

Of the sixteen most characteristic calcicole species examined, eleven¹ have

¹ *Ajuga chamaepitys*, *Anemone pulsatilla*, *Asperula cynanchica*, *Gentiana amarella*, *Linum catharticum*, *Ophrys apifera*, *Teucrium botrys*, *Filipendula hexapetala*, *Bromus erectus*, *Chlora perfoliata* and *Avena pubescens*.

a maximum penetration of from 3·2 to 6 in., four¹ show a maximum penetration of from 12 to 34 in., whilst *Carlina vulgaris* has a maximum penetration of 8·8 in.

Group A.

Ajuga chamaepitys (4 plants examined).

Average working depth, 1–2 in.; maximum penetration, 3·2 in.; average spread, 1·8 in.

The specimens occurred on a shallow bed of gravel overlying the chalk, they possessed a sturdy whitish root system with but few branches and a tap root distinguishable throughout. The root hairs were few and scattered, and no mycorrhizal filaments appeared to be associated with the root system.

Anemone pulsatilla (3 plants examined).

Average working depth, 0·5–2·5 in.; maximum penetration, 3·5 in.; average spread, 2·5 in.

The specimens occurred on a soil similar to that described on p. 73.

There is a strong woody rhizome about 1·5 in. below the surface of the soil which gives off a number of adventitious roots with a smooth brown cork and only very occasional branches. The outer layer appears to be suberised from the tip of the root, and no root hairs were observed. Hyphae showing clamp connections were found outside the root and associated with the outer cortical cells.

Asperula cynanchica (4 plants examined from Farthing Down).

Average working depth, 0–1·5 in.; maximum penetration, 6 in.; average spread, 7·5 in.

This plant possesses a strongly-developed system of red-brown wiry roots in the surface layer of soil, these have a soft cortex which appears to disintegrate very readily, after which it often becomes associated with fungal hyphae. Root hairs are not abundant, averaging 4 per 0·1 mm. at a depth of 1 in. but on the finer rootlets nearer to the surface there were on an average 12 per 0·1 mm. Septate root hairs were seen in several instances.

One or more anchoring roots were found on each plant, penetrating to a depth of 5 or 6 in.; these bore only a very occasional hair, but fungal hyphae were more abundant than on the upper roots.

Avena pubescens (6 plants examined).

Average working depth, 0–2·5 in.; maximum penetration, 4·5 in.; average spread, 5 in.

This plant has a luxuriant crop of white fibrous roots well branched and forming a dense network in the soil occupied. The root hairs were well developed and abundant, occurring from the very short meristematic region at the tip upwards for about an inch, after which they become disintegrated. Fungal hyphae were present around the roots but no connection was traced.

Bromus erectus (6 plants examined).

Average working depth, 0–3 in.; maximum penetration, 5 in.; average spread, 4 in.

¹ *Anthyllis vulneraria*, *Hippocrepis comosa*, *Poterium sanguisorba*, *Scabiosa columbaria*.

A very large number of brown fibrous roots are produced radiating in every direction from the crown, and bearing a few laterals. The roots are well provided with hairs throughout their length, and, although in places fungal filaments were entangled with the hairs, they did not appear to be present in any part of the cortex.

Chlora perfoliata, Fig. 9 (17 plants examined from chalk).

Average working depth, 0-3.5 in.; maximum penetration, 5.3 in.; average spread, 2.5 in.

A white and somewhat fleshy root system in which the main axis is generally conspicuous for about half its extent; in relation to the size of the plant the system is somewhat poorly developed. The root hairs chiefly occur in scattered

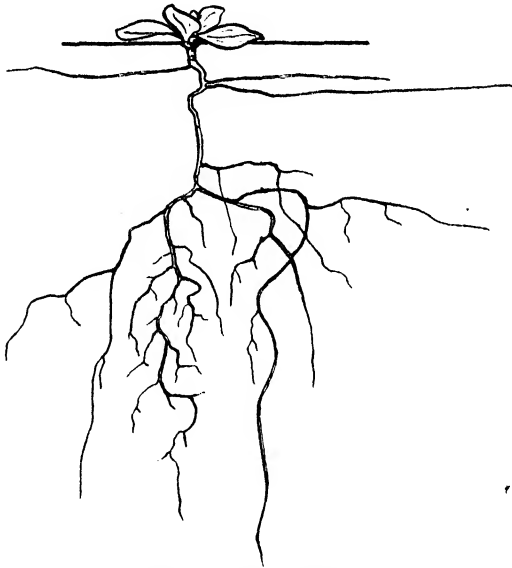


FIG. 9. *Chlora perfoliata*. $\frac{2}{3}$ Natural size.

zones some 0.5 cm. long and in these patches they are very numerous; local thickened yellowish zones occur behind these, and were seen to be the seat of concentrated mycorrhizal infection, and the broken-down root hairs found at such places seemed to show a certain relation between the root hair and fungal zones.

A characteristic feature of these root systems was the presence of one, two or three long, delicate and unbranched roots given off from the main root just below the surface of the soil and running out horizontally; these were practically without root hairs nor were any fungal hyphae associated with them.

Cephalanthera pallens (3 plants examined from shallow soil, solid chalk at depth of 6 in.). This is a woodland, not a chalk grass-land plant.

Average working depth, 3-4.5 in.; maximum penetration, 6 in.; average spread, 3.5 in.

No tuber was present; from the stem base, some 3 in. below the surface of the ground, 8-10 thick fleshy roots were given off diagonally. Root hairs were abundant and most of the cells of the cortex contained mycorrhizal fungi in typical masses.

Fragaria vesca, Fig. 10 (6 plants examined). This woodland species is locally abundant on chalk grass land.

Average working depth, 2-4.5 in.; maximum penetration, 6.5 in.; average spread, 4.5 in.

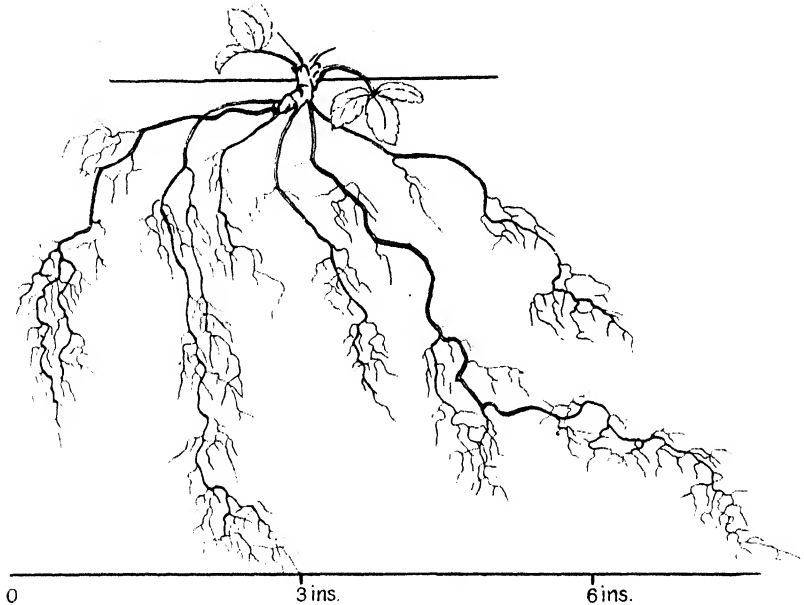


FIG. 10. *Fragaria vesca*. $\frac{1}{2}$ Natural size.

The root system is coarse and fibrous, and in relation to the size of the plant is abundantly developed. The root hairs are not abundant and are very irregularly distributed, and while 1 mm. may be destitute of hairs the next may bear 35-40. Fungal hyphae are usually abundant and appear to be definitely associated with the cortical cells.

Gentiana amarella, Fig. 11 (10 plants examined).

Average working depth, 0.5-3 in.; maximum penetration, 4 in.; average spread, 1.5 in.

The root system is a bright yellow in colour with local tendencies to become greenish. The tap root is generally distinguishable throughout its length and both this and the few laterals are thick and strongly developed in relation to the size of the plant. The laterals are given off at wide angles. Very few root hairs occur, averaging 3 per 1 mm., but a most luxuriant crop

of root hairs developed on specimens grown in water for 6 weeks. No fungal hyphae appeared to be present on the majority of plants examined, but three had several areas on the upper laterals where fungal filaments appeared to be associated with cells of the outer cortex.

Hieracium pilosella (10 plants examined).

Average working depth, 1-3 in.; maximum penetration, 4.5 in.; average spread, 4 in.

Since the plant tends to occur in patches, spreading by vegetative means, the spread of a single root system is apt to vary considerably according to the

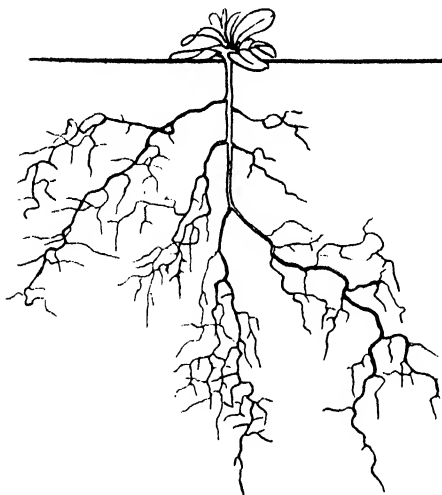


FIG. 11. *Gentiana amarella*. $\frac{3}{4}$ Natural size.

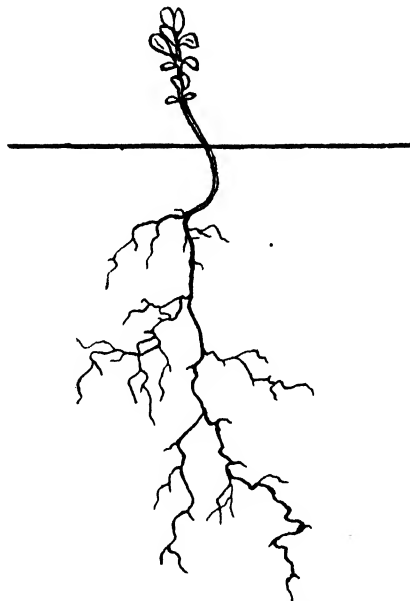


FIG. 12. *Linum catharticum*. Natural size.

degree of disintegration of the older parts of the rhizome; the latter is a strong and slightly swollen organ bearing some 10-20 rather coarse white roots (2-3 in. long) which travel diagonally through the soil and have but a few small branches. Many of these branches were destitute of root hairs, while no part of the root system had an average of more than 12 root hairs per 1 mm. Fungal hyphae were abundant around the root and between the cells of the cortical region, in several instances the hyphae appeared to be associated with the root cap itself.

Linum catharticum, Fig. 12 (12 plants examined).

Average working depth, 0.5-3 in.; maximum penetration, 4 in.; average spread, 2 in.

The root system is a very delicate and well-branched structure, the main axis being readily distinguished for about half the extent of the root system. The root hairs are fairly evenly distributed and average 60 per 1 mm.; they

may appear almost at the tip itself and appear to be well established in the region immediately behind, and may be found, though in less abundance, right back to the base of the stem. Fungal filaments were seen between the cortical cells and dark spore masses were also detected here in two instances. The hyphae were more abundant in slightly yellowish zones.

Ophrys apifera, Fig. 13 (25 plants examined).

Average working depth, 1-3 in.; maximum penetration, 3-5 in.; average spread, 1-8 in.

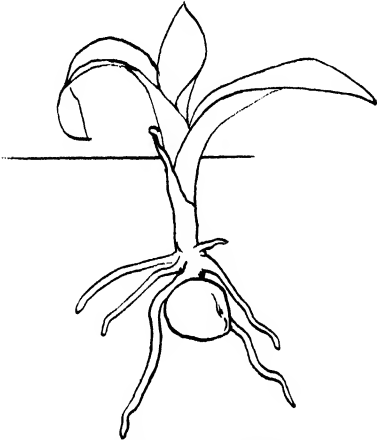


FIG. 13. *Ophrys apifera*. $\frac{1}{2}$ Natural size.

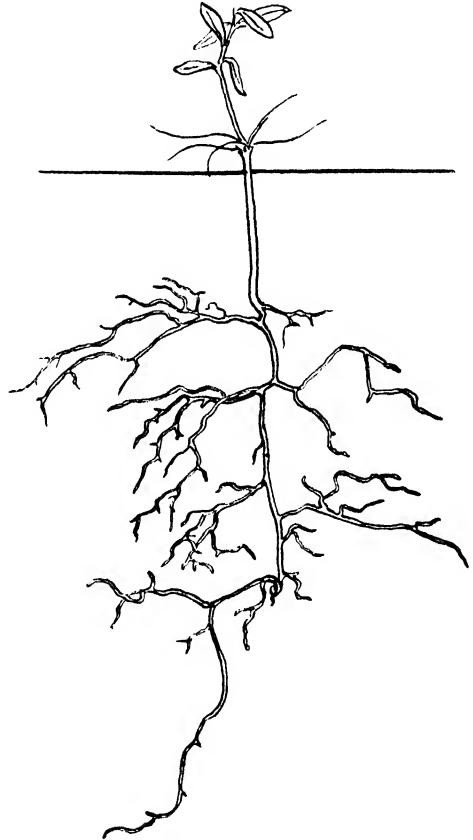


FIG. 14. *Polygala vulgaris*. $\frac{2}{3}$ Natural size.

The most conspicuous feature of this root system is the large white fleshy tuber, more or less egg-shaped, from the crown of which arise 3-7 thick fleshy white roots, unbranched and brittle. The new tuber arises in early spring alongside the old one, which is exhausted by flowering time. The endotrophic mycorrhiza is too well known to require description here, but it may be noted that the process of infection *via* a root hair was frequently seen. The root hairs are fairly evenly distributed and average 110 per mm.

Polygala vulgaris, Fig. 14 (10 plants examined).

Average working depth, 1-3 in.; maximum penetration, 5 in.; average spread, 2.5 in.

This has a system of sturdy white roots, the main axis usually remaining distinguishable throughout its length and the laterals given off at wide angles. There are only very few root hairs, never more than 5 per 1 mm., and many of the young laterals are quite destitute of hairs. Distally many of the roots bear zones of endotrophic mycorrhiza, and here the plant would seem to respond by casting off the outer cortical layers.

Plantago lanceolata, Fig. 15 shows a specimen with exceptionally deep roots from a loose chalk cliff.

Six plants were examined from the chalk down and these had an average working depth of 1.5-3 in.; maximum penetration, 5.5 in.; average spread, 3 in.

Numerous roots are given off from an oblique and sturdy rhizome. The roots are but slightly branched, but the root hairs are abundant and well distributed. Occasional fungal hyphae were seen and they appear to ramify on and between the outer cells of the root.

Spiraea filipendula (*Filipendula hexapetala*), Fig. 16 (6 plants from Farthing Down examined).

Average working depth, 1.5-3.8 in.; maximum penetration, 5 in.; average spread, 3.5 in.

The plant has a very characteristic root system; the main axis divides into two or three strong dark brown limbs about 1 in. below the surface. The main laterals bear swellings nearly as large as an

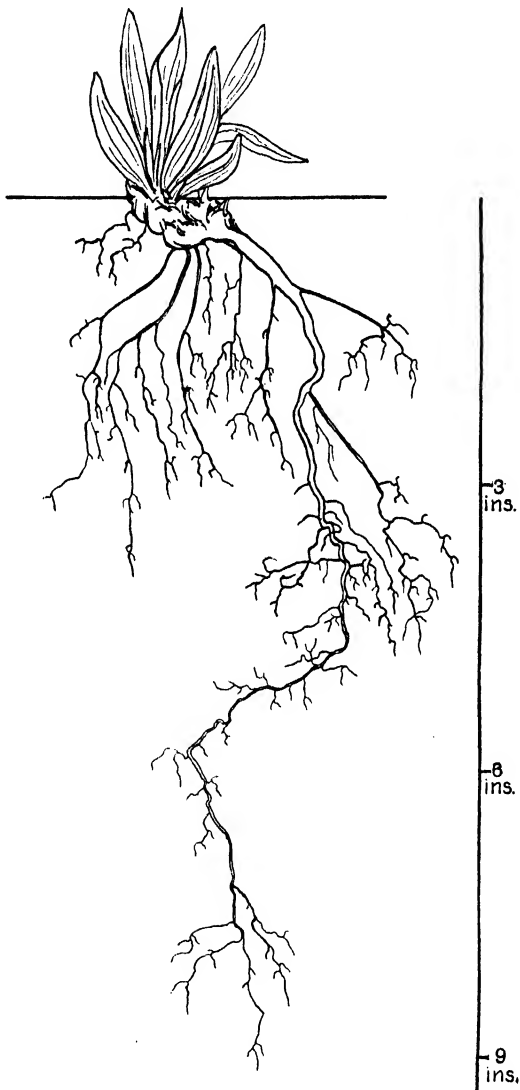


FIG. 15. *Plantago lanceolata* from a much fissured chalky cliff at Folkestone. The root development is greater than was found to occur on the open down. $\frac{1}{2}$ Natural size.

acorn towards their distal ends, and while starch is practically absent from the normal portions of the root, the swellings are richly stored with it. A few small secondary laterals are produced, which may branch sparingly, but all seem to have a brown corky covering which may account for the fact that no root hairs were seen on any part of the system. A very few hyphae were found to be present, being detected between some of the outer cells when the roots were teased out.

Teucrium botrys (4 plants examined from shallow gravel overlying chalk).

Average working depth, 1-3 in.; maximum penetration, 4.5 in.; average spread, 1.5 in.

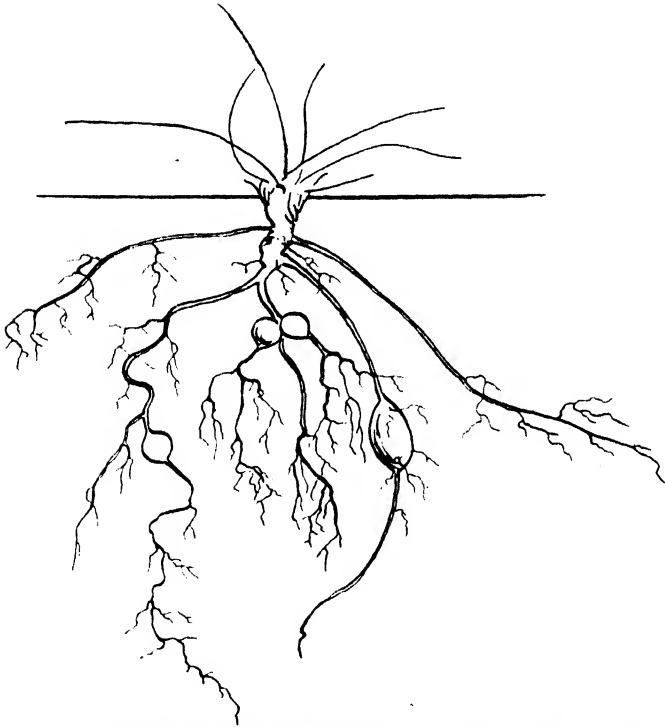


FIG. 16. *Spirea filipendula* (*Filipendula heurapetala*). $\frac{2}{3}$ Natural size.

There is a sturdy but poorly branched system with a distinct tap root. The root hairs were evenly distributed and frequent, averaging 85 per 1 mm. No mycorrhizal fungi were observed.

Viola hirta (6 plants examined).

Average working depth, 0.5-4 in.; maximum penetration, 6.3 in.; average spread, 3.5 in.

This has a strongly developed system, with numerous white roots arising from a stout rhizome obliquely placed in the soil and apparently much contracted.

The adventitious roots may be 3-4 in. long and are richly branched. The root hairs, which are short and rather thick walled, are unevenly distributed, averaging 220 per mm. Occasional fungal hyphae appeared to be associated with the roots, although the latter were mostly free from fungi.

Group B.

Achillea millefolium (6 plants examined).

Average working depth, 2-4.5 in.; maximum penetration, 8.5 in.; average spread, 3.5 in.

Adventitious roots some 2-3 in. in length are given off from a rhizome which is more or less horizontal in the soil, and which in a loosely knit chalk soil is more deeply buried than in a compact one. Root hairs are frequent, well developed and evenly distributed, and fungal filaments, though few in number, appeared to be associated with the roots.

Anthyllis vulneraria, Fig. 17 (15 plants examined).

Average working depth, 3-8 in.; maximum penetration, 12.5 in.; average spread, 3 in.

This root system showed a wider range of variation than that of any other plant considered in the present investigation. In one instance the main tap root (13 in. long) was the chief feature and bore but five scattered laterals all less than 4 in. long; the spread was not greater than 2.5 in. in any direction from the crown. Another plant growing less than 6 ft. away had no clearly defined tap root, since the main axis divided into three parts within $\frac{1}{2}$ in. from the soil surface, and a well-branched root system was formed with a spread of 4.4 and 5 in. in different directions, the maximum penetration in this instance being only 5 in. The number of bacterial nodules varied considerably with different plants. No fungal hyphae were seen, the root hairs were abundant on the younger parts of the roots, averaging as much as 350 per 1 mm., but they would not appear to persist for long, and none of healthy appearance were seen more than 4 cm. from the root tip.

Carlina vulgaris, Fig. 18 (6 plants examined).

Average working depth, 1.5-6 in.; maximum penetration, 8.8 in.; average spread, 2.5 in.

The root system consists of a fleshy tap with a few coarse laterals; the root hairs were very few in number and unevenly distributed and no mycorrhizal filaments were observed.

Cirsium acaule (6 plants examined).

Average working depth, 2.5-6 in.; maximum penetration 9.5 in.; average spread, 2.5 in.

A thick and fleshy white tap root is characteristic, but it may divide at an early stage into two or three limbs; it bears a few scattered fine laterals, seldom more than 1.5 in. long. Root hairs are of rare and local occurrence,

averaging 2 per 1 mm. root. A few hyphae were found around the outer cell layer, but no penetration was seen.

Daucus carota, Fig. 19 (6 plants examined).

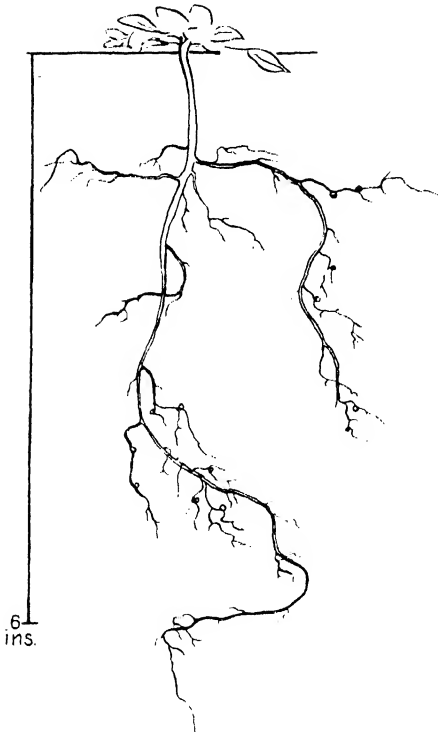


FIG. 17. *Anthyllis vulneraria*. $\frac{1}{2}$ Natural size.

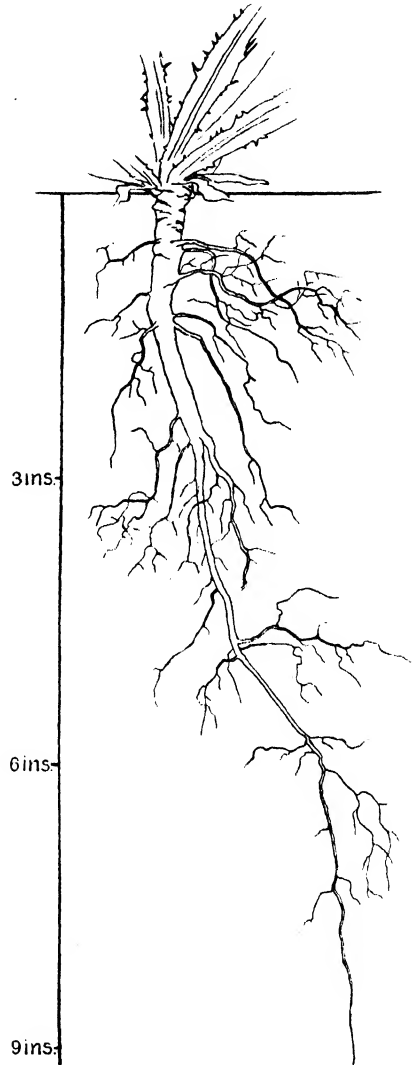


FIG. 18. *Carlina vulgaris*. $\frac{1}{2}$ Natural size.
From a loose chalk cliff at Folkestone.

Average working depth, 4.5–9 in.; maximum penetration, 13.5 in.; average spread, 2.5 in.

A well-marked fleshy tap root is always present, bearing a few short feeding roots in the upper 4 in. of soil, but they then become more numerous with increasing depth. Root hairs are chiefly confined to a zone extending

from 7 to 12 mm. from the tip of the root, where they are evenly distributed although not very abundant (40 per 1 mm.). Fungal hyphae were very numerous around the finer roots and appeared to be associated with the cortical cells.

Helianthemum chamaecistus (4 plants examined).

Average working depth, 0-5 in.; maximum penetration, 10-5 in.; average spread, 14 in.

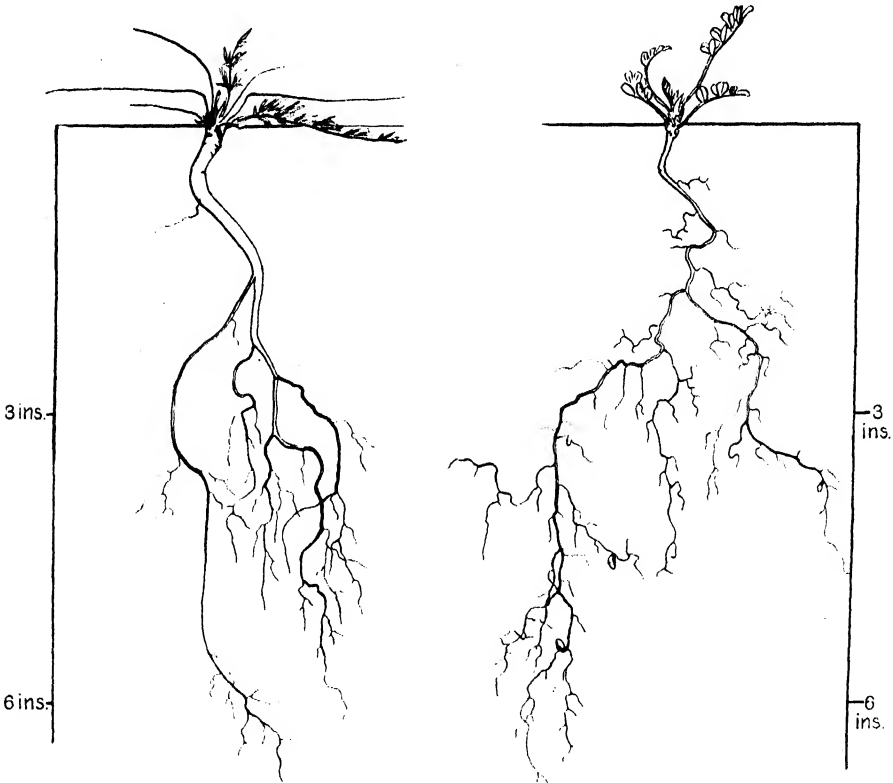


FIG. 19. *Daucus carota*. $\frac{1}{2}$ Natural size.

FIG. 20. *Hippocrepis comosa*. $\frac{1}{3}$ Natural size.
From a loose chalk cliff at Folkestone.

The plant has a dark brown wiry root system with a number of coarse branches, effectively occupying the top few inches of soil. Each plant pushes down one or more anchoring roots. No root hairs were seen; fungal hyphae were abundantly associated with a brown outer layer of the cortex which appeared to be readily shed.

Hippocrepis comosa, Fig. 20 (5 plants examined).

Average working depth, 4-8 in.; maximum penetration, 12-5 in.; average spread, 3 in.

This root system may vary considerably, but the tap root is generally strongly developed, the laterals being of somewhat fine texture and very

irregularly branched. Root hairs were abundantly developed in local patches on the laterals, in some places as many as 560 per 1 mm. The roots were free from fungal infection except in two cases where groups of cortical cells appeared to harbour mycelium, and in the same region free fungal filaments were interwoven among the root hairs.

Lotus corniculatus (6 plants examined).

Average working depth, 3-7.5 in.; maximum penetration, 12 in.; average spread, 5.5 in.

The tap root may be as much as 18 in. long, but it may often run obliquely for the first few inches and is often somewhat contorted in the region where it encounters the transition from the broken chalk to the more solid rock. Root hairs were only occasional on the upper part of the root but were more numerous on the lower parts. No fungal infection was seen.

Medicago lupulina, Fig. 21 (7 plants examined).

Average working depth, 2.5-5.5 in.; maximum penetration, 10.5 in.; average spread, 4 in.

A tap root is usually distinguishable for the greater part of the root system, the laterals being plentiful and strongly developed. The bacterial nodules are mostly near the soil surface, and here there is no fungal infection. At a depth of about 7 in. fungal hyphae occur and appear to make their way between the cortical cells in a few zones. The root hairs are

few in number and very unevenly distributed. The root tips near the surface taper to a much finer point than those which are deeper.

Origanum vulgare (4 plants examined).

Average working depth, 1-4 in.; maximum penetration, 8.5 in.; average spread, 6.5 in.

A fibrous mass of roots is produced, most strongly developed some 2-3 in. below the surface, with an occasional limb striking downwards. The root hairs are very long and numerous, beginning close behind the tip, where they are best developed; as they do not appear to persist for long, healthy

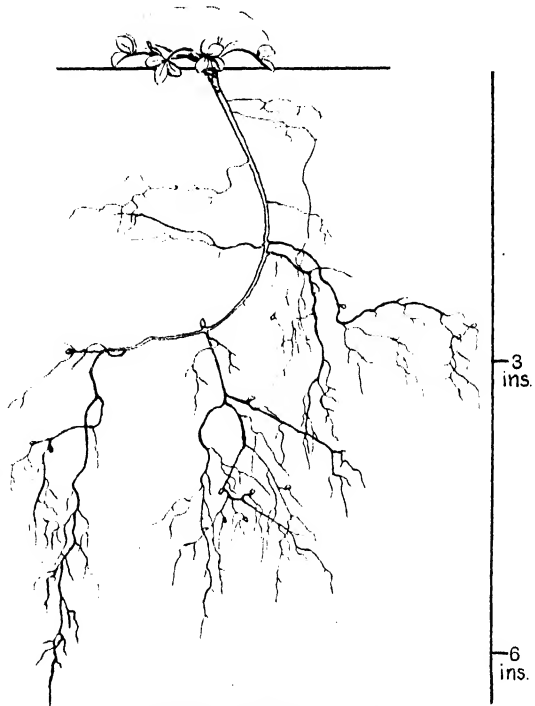


FIG. 21. *Medicago lupulina*. $\frac{1}{2}$ Natural size.

looking hairs are rarely seen more than 2.5 cm. from the tip. Fine fungal hyphae with occasional septa occur locally and appear to be associated with the cortical cells.

The merismatic region of the root is very short and the tip blunt.

Pastinaca sativa, Fig. 22 (9 plants examined).

Average working depth, 2.5–7 in.; maximum penetration, 14.5 in.; average spread, 4 in.

A thick white tap root is usually the chief feature of this root system, and is especially well developed when the plant occurs in a loose chalky soil such as may frequently be found on the site of an old rabbit warren; but where the plant occurs on a shallow soil with the solid chalk rock near the surface the root system is apt to be distorted, the roots avoiding the solid rock, and

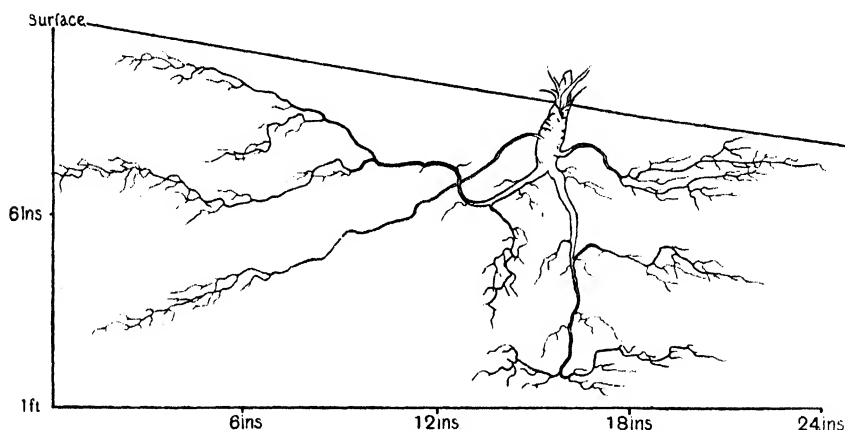


FIG. 22. *Pastinaca sativa*, growing on sloping ground. $\frac{1}{3}$ Natural size.

the tap may become divided into several limbs which radiate in the loose subsoil. In one instance the tap root had grown vertically upwards for $4\frac{1}{2}$ in. thus overcoming the need to penetrate into the crevices of the chalk. The merismatic region of the root is longer than in most of the plants examined, and no root hairs occur within 2 mm. of root tip. The hairs are few in number and scattered. No fungal infection was observed.

Plantago media, Fig. 23 (5 plants examined).

Average working depth, 1.5–4.5 in.; maximum penetration, 7.5 in.; average spread, 2 in.

The tap root is well developed and bears numerous fine laterals. The root hairs are long and abundantly developed close behind the tips, but they soon decrease in numbers and are mostly disintegrated 2 cm. from the tip, in which region there tends to be a breaking down of the outer cortical regions of the root, and here, too, fungal hyphae are much in evidence.

Potentilla reptans (4 plants examined).

Average working depth, 2-6 in.; maximum penetration, 8 in.; average spread, 1.5 in.

A strong descending root appears to be pushed down each season, and develops a few laterals. Very few root hairs occur, 4 per mm. on younger roots and none on the older parts, which develop a suberised outer layer. Hyphae were seen around the root in several instances, but no definite association appeared to exist.

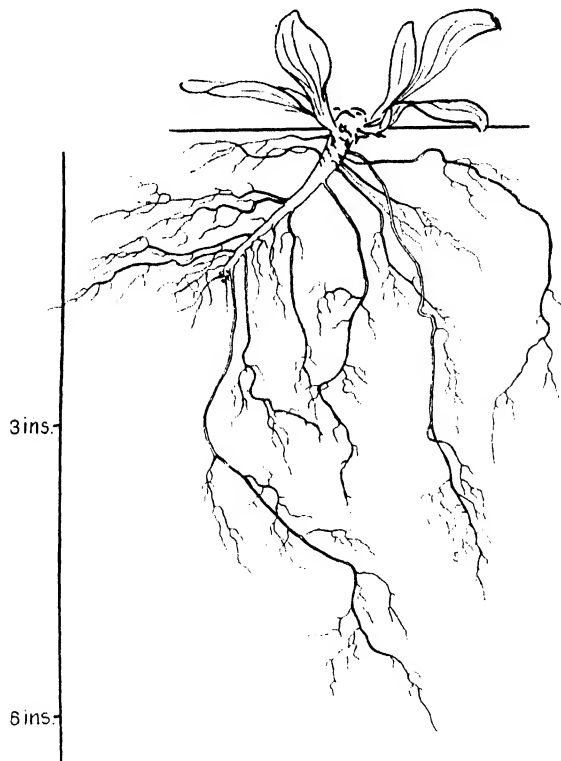


FIG. 23. *Plantago media*. $\frac{1}{2}$ Natural size.

Primula veris (6 plants examined).

Average working depth, 6-10 in.; maximum penetration, 11 in.; average spread, 1.5 in.

The rhizome is buried some 4-5 in. below the surface of the soil, and bears a number of thick white fleshy roots some 4-5 in. long. These are but very scantily branched, and the laterals are very fine and fibrous. Root hairs are fairly abundant, but are very small: they arise close behind the growing tip (70 per 1 mm.) and are scattered on all the laterals. Fungal hyphae of very fine filaments occur and appear to be associated with the cortical cells of the finer roots.

Sonchus arvensis (3 plants examined).

Average working depth, 4–7 in.; maximum penetration, 12.5 in.; average spread, 3 in.

A white and rather soft root system in which the tap is usually distinguishable for the upper half. Fungal hyphae are abundant on all parts of the root but there are only a few large root hairs (3 per 1 mm.), none nearer the tip than 2 mm.

Verbascum thapsus (3 plants examined).

Average working depth, 0–3 in.; maximum penetration, 11 in.; average spread, *cir.* 18 in.

One or more anchoring roots bearing a few branches are present, but the chief feeding roots occur just below the surface of the ground on 3–5 long and richly branched laterals of fine texture. In a patch of chalk scrub disturbed by rabbits and with a very loose surface soil these had a maximum spread of 39 in. On the open down technical difficulties, chiefly the delicacy of the roots, prevented the detection of a spread of more than 18 in. from the crown. Root hairs were only few and scattered, but fungal filaments were much in evidence around the roots.

Group C.

Galium verum, Fig. 24 (3 plants examined).

Average working depth, 15–24 in.; maximum penetration, 30 in.; average spread, 4 in.

A long thin tap root practically unbranched above but bearing numerous laterals of fine texture below, these being localised in the crevices of the chalk. Root hairs occur in patches on the younger parts of the root, but are gradually replaced by fungal hyphae, which are locally plentiful.

Hypericum perforatum, Fig. 25 (5 plants examined).

Average working depth, 6–17 in.; maximum penetration, 24 in.; average spread, 5 in.

One or more strongly descending roots are given off from the root stock just below the surface of the ground, and these bear a number of thread-like and branched laterals. Very few root hairs were observed (average less than 1 per 1 mm.) but fungal hyphae were abundant in and around the cortex which appeared to disintegrate very readily.

Onobrychis sativa, Fig. 26 (4 plants examined).

Average working depth, 7–16 in.; maximum penetration, 23 in.; average spread, 4 in.

The system is characterised by a strong brown tap root, sometimes obliquely placed, bearing only a few laterals of coarse texture and these being confined to the lower part; bacterial nodules were small. Very few root hairs were seen and no fungal filaments.

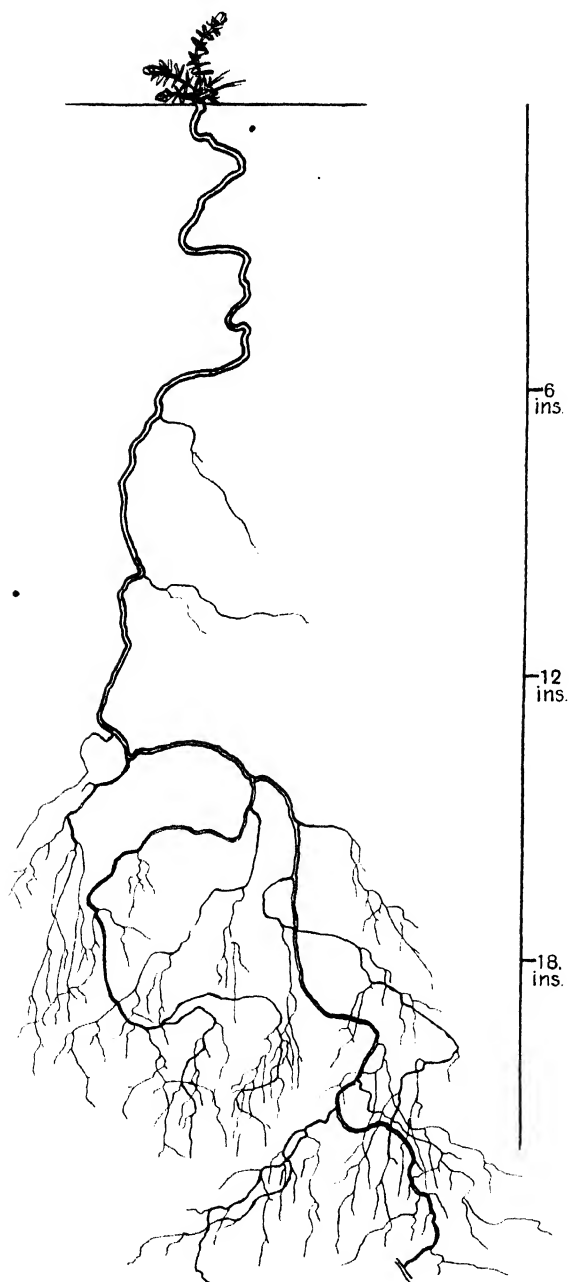


FIG. 24. *Galium verum*. $\frac{1}{4}$ Natural size.

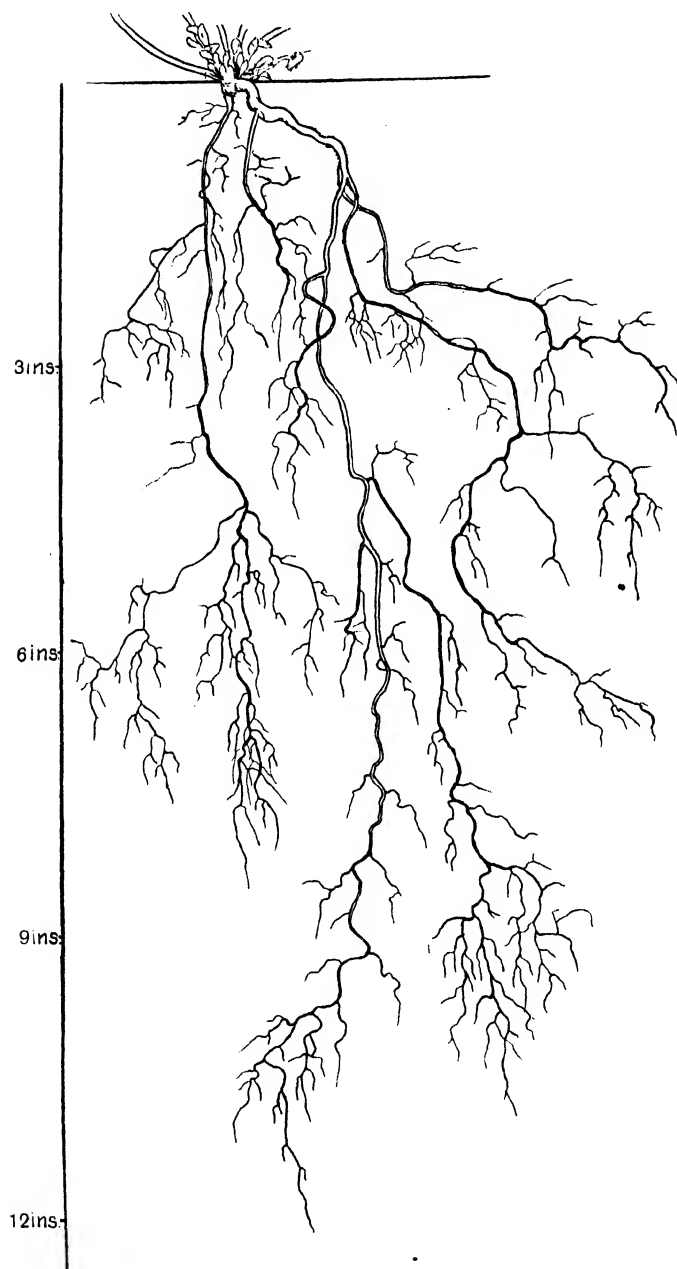


FIG. 25. *Hypericum hirsutum*. $\frac{1}{2}$ Natural size.
From a loose chalk cliff at Folkestone.

Ononis spinosa (3 plants examined).

Average working depth, 18-28 in.; maximum penetration, 37 in.; average spread, 5 in.

This plant had the deepest root system of any examined, with a well-developed woody tap sometimes practically unbranched for the first 20 in., then producing 4-7 laterals, which ramify considerably in the crevices of the chalk, and distally are richly clothed in root hairs for a distance of 8-10 mm. from the tip. No fungal hyphae were observed.

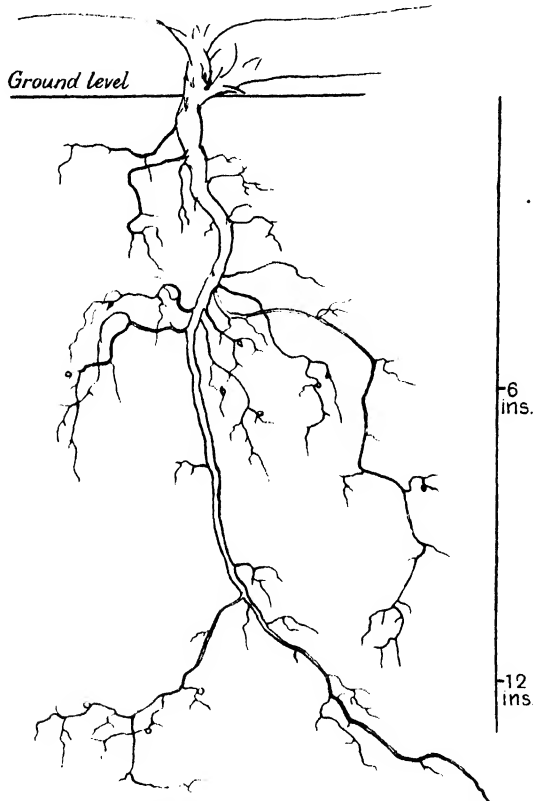


FIG. 26. *Onobrychis sativa*, young plant with root system not yet fully developed. $\frac{1}{4}$ Natural size.

Poterium sanguisorba, Fig. 27 (23 plants examined).

Average working depth, 16.5-27 in.; maximum penetration 34 in.; average spread, 4 in.

This perennial has a woody dark brown tap root and shows a good range of variation both as regards the depth and branching of the roots. In 15 of the plants examined no significant branches occurred on the tap root to a depth of 12 in. or more, but the tap may bear a lateral of considerable size at a depth of 3.5 in. In the chalk rock considerable branching occurs and a

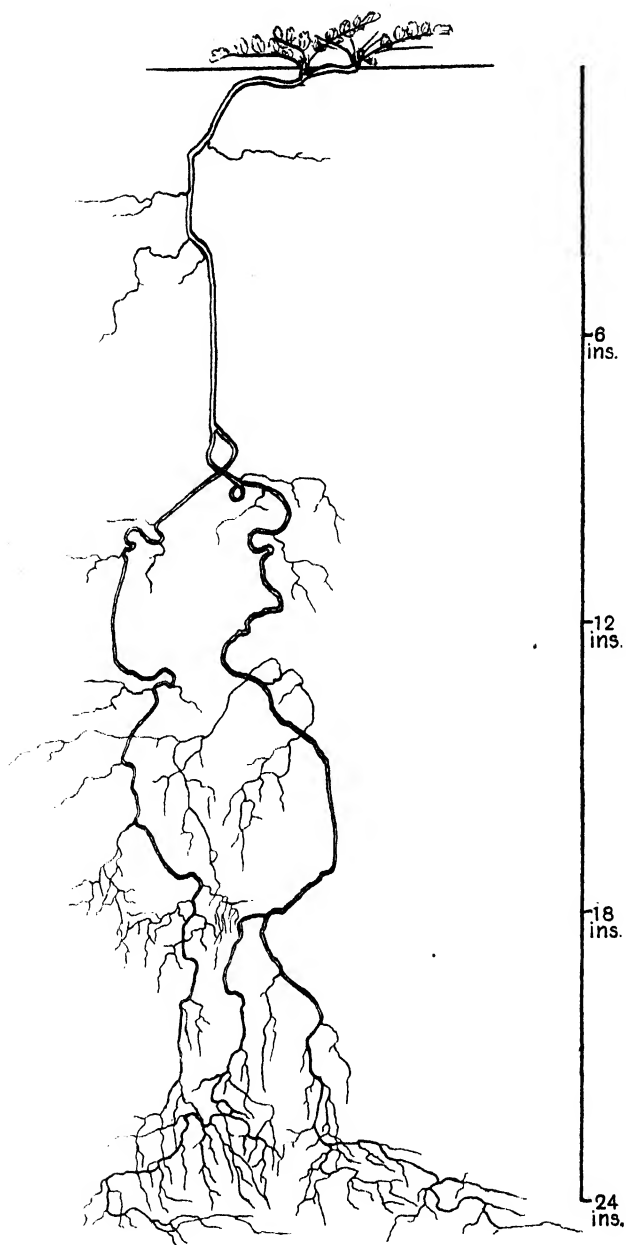


FIG. 27. *Poterium sanguisorba*. $\frac{1}{4}$ Natural size.

richly developed ramification of rootlets in the crevices. A number of seedlings were also examined; they had delicate fibrous roots and only began to show the characteristics of the adult type when they had attained a depth of some 6 in.

Root hairs are well developed on all the lateral roots, more particularly the lower ones, on some of which there may be as many as 300 per 1 mm. on the distal 3 cm. of root; behind this they tend to disintegrate somewhat rapidly. Fungal hyphae were observed occasionally around the roots, but there was probably no definite association.

Reseda luteola (3 plants examined).

Average working depth, 6.5–14 in.; maximum penetration, 17 in.; average spread, 5 in.

This plant has a tap root the upper part of which is markedly contractile, and below this region at a depth of some 3–4 in. it tends to divide; a few coarse whitish laterals are produced. The root tips were very blunt; no root hairs were observed, but there were a few fungal hyphae evidently in association with the upper laterals.

Scabiosa columbaria (7 plants examined).

Average working depth, 7–17 in.; maximum penetration, 23 in.; average spread, 5 in.

A very abundant root system is characteristic of this plant; the identity of the tap root is soon lost in the large number of whitish laterals which form a mat in the fissures of the chalk, but when an appreciable leached layer of soil exists above the chalk the root system becomes more elongated and is but poorly branched in the upper part. Root hairs were abundant, but very irregularly distributed, and confined to the ultimate 6 cm. or so of root. Fungal hyphae also occurred on the upper laterals but not on the deeper ones.

Silene inflata (5 plants examined).

Average working depth, 6–14 in.; maximum penetration, 34 in.; average spread, 7 in.

The crown of the plant is buried several inches deep in the soil and from this one or more strong descending roots arise. The laterals are mostly of small diameter, but little branched, and of a remarkably frail texture. The outer cortical layers of these roots break up very readily, giving an impression of inefficiency, particularly as filamentous fungi find a suitable home there. The root tips are blunt and slightly swollen, with a few root hairs almost at the tip itself and immediately behind it.

Thymus serpyllum (7 plants examined).

Average working depth, 0–4 and 12–20 in.; maximum penetration, 28 in.; average spread, 6 in. at surface, 4 in. at 20 in.

This plant has an irregular root system of branched and wiry brown roots a few inches below the surface. One or more strong descending roots are given off and penetrate into the solid rock below, there producing a large

number of fine branches ramifying in the chalk crevices; these develop a dense growth of root hairs in the first 10 mm., but they soon break down. On the surface root hairs are very few and local (8 per 1 mm.), fungal hyphae are present on these rootlets, abundantly on most of them, but they do not appear to occur on the deeper roots.

A few seedlings of woody plants typical of the chalk have been examined, and in general these were found to have very abundant root systems, similar to each other in type, and all well supplied with root hairs. The seedlings

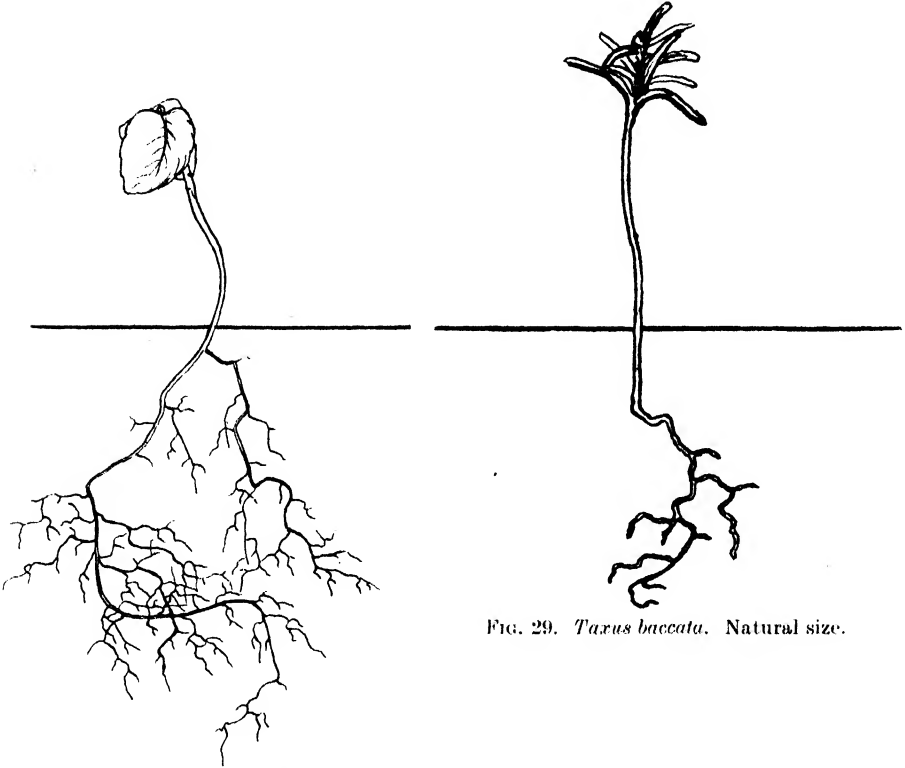


FIG. 28. *Viburnum lantana*. $\frac{2}{3}$ Natural size.

FIG. 29. *Taxus baccata*. Natural size.

considered were those of *Viburnum lantana* (Fig. 28), *Taxus baccata* (Fig. 29), *Ligustrum vulgare* (Fig. 30). Young *Cornus sanguinea* plants were also found to have well-developed root systems, but no seedlings were found, and reproduction appears to be commonly vegetative, by means of axes some 3 or 4 in. below the surface of the ground and as much as 7–10 ft. long.

(a) VERTICAL DISTRIBUTION OF ROOTS.

Reference to the diagrams, Figs. 7 and 8 (pp. 89, 90), will show the maximum rooting depth attained by individual plants, the heavy lines indicating the

average working depth, i.e. the zone at which the chief feeding roots usually occur for a given species.

As has already been mentioned, the grasses are among the more shallow-rooted types; a few, such as *Bromus erectus* or *Brachypodium pinnatum*, may penetrate to a depth of 4 in. or more but the bulk of the feeding roots are restricted to the top 2 or 3 in. of soil. Group A includes a number of perennials such as *Anemone pulsatilla*, *Polygala vulgaris* and *Asperula cynanchica*, the last

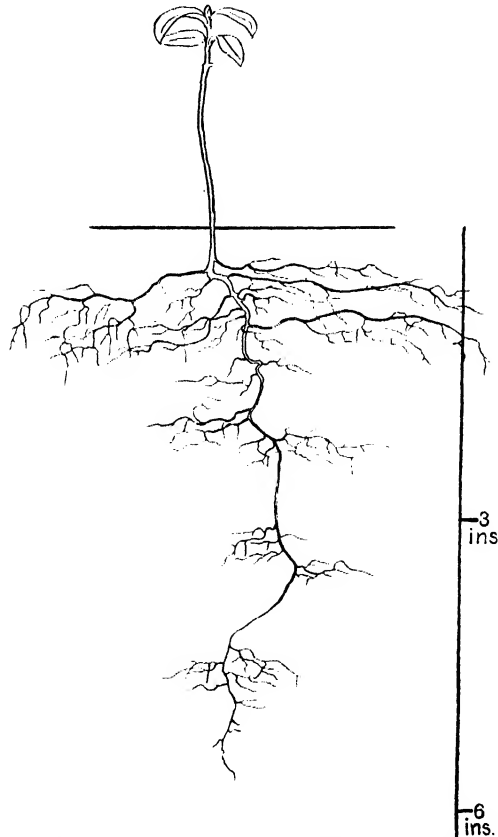


FIG. 30. *Ligustrum vulgare*. $\frac{1}{2}$ Natural size.

having a particularly shallow system. There are also in this group some of the more characteristic annuals such as *Gentiana amarella*, as well as *Chlora perfoliata* and *Linum catharticum*, which are usually winter annuals.

All these plants appear to be but poorly equipped as regards extent of root systems, when they are compared with the grasses with which they must compete; and it is only seldom that plants whose roots are confined to this zone can hold the grasses in check both above and below ground, or offer a serious opposition to their dominance; *Hieracium pilosella* is perhaps the most

successful and this is rather a plant of any dry soil than a typical member of the chalk down community. Both *Chlora perfoliata* and *Thymus serpyllum* possess, in addition to the main ramifications of their root systems, roots which tap the surface inch of soil, and in view of the fact that this upper zone of the soil may have its water content frequently augmented by deposition of dew at a time of water scarcity, it is possible that these surface roots may be of considerable importance (see p. 77). An even more marked development of surface roots occurs in *Verbascum thapsus*, in which the deeper roots are comparatively poorly developed.

In the roots of the plants of Group A there is a great variety of type; thus the grasses have mostly a wealth of very fine fibrous roots; *Polygala vulgaris* (also *P. calcarea*), *Teucrium botrys* and *Gentiana amarella* have systems with fairly well defined tap roots; while in *Plantago lanceolata*, *Viola hirta* and *Anemone pulsatilla* the roots are borne on well-developed rhizomes or root stocks; in the last mentioned, as in *Spiraea filipendula*, the root systems are woody and protected by an early and extensive formation of cork, while to all these forms, a vivid contrast is offered by the fleshy underground parts of *Ophrys apifera* with four or five short unbranched roots and an ovoid tuber. In neither of the other groups is there to be found an equivalent range of type.

While this wide range of type is represented in Group A it is particularly noteworthy that the range of variation within the species is very much smaller than in either of the other groups, and indeed in some species, e.g. *Chlora perfoliata*, the branching is remarkably uniform, when growing on the chalk. Some plants of *Chlora* were found on a water-logged calcareous clay on the north of the Isle of Wight, these proved to have root systems much less strongly developed and of a finer texture than those which grew on the chalk. *Polygala vulgaris* on the chalk develops a root system which is intermediate in type between that which it develops on shingle and on clay. On the beach at Pevensey *Polygala* was found to develop a sturdy and woody root system with a corky covering much more extensive than the roots of a chalk plant, and with a maximum penetration of 7 in. In the heavy and wet clay on the north of the Isle of Wight the plants were found to have very poorly developed root systems with thin and thread-like limbs and a maximum penetration of 3 in.

The second group of plants, those of which the roots have a maximum penetration ranging approximately from 6 to 12 in., consist mostly of perennials, and amongst the plants of this group there may be a very considerable range of variation for the root of a given species; although the range of type found in the group as a whole is much smaller than for the more shallow-rooted plants.

The roots of the legumes and more particularly of *Anthyllis vulneraria* are particularly variable, so that there is no really central type of root for this species (see special description, p. 98), and it would be interesting to know

whether this variability is in any way to be correlated with other features common to the roots of these leguminous plants.

Pastinaca sativa is also very variable, but here the variability seems to be a direct response to soil structure, the roots avoiding the solid chalk as described on p. 102, so that a highly distorted system sometimes results.

The more deeply rooted plants of Group C are mostly characterised by the possession of tap roots which, as in the case of *Ononis*, may penetrate to a depth of 3 ft. with *Poterium* a good second going to 30 or even 34 in.

While there is still a wide range of variation, the plants of this group tend to conform more to a given type for each species than do those of the previous group, and this may probably be accounted for by the fact that a good many soil conditions, such as texture and chemical composition, are more constant in the second foot below the surface than in the first. Thus, out of 23 adult plants of *Poterium sanguisorba* examined, 15 had no significant laterals for the upper 12 in., and in all cases the distal parts consisted of fine thread-like and brittle rootlets lying in the planes of the chalk crevices.

Reviewing the whole range of root systems examined, there is found no obvious correlation, either positive or negative, between the depth of penetration (either average or maximum) and the extent of radial spread of the lateral roots. In a number of instances an attempt was made to calculate the volume of soil exploited by the roots of certain species, and the figures recorded below (Table VI), although only approximately correct, will afford a rough basis of

Table VI. *Volume of Soil exploited by Root Systems.*

	Cub. in.		Cub. in.
<i>Ajuga chamaepitys</i>	20	<i>Asperula cynanchica</i>	265
<i>Ophrys apifera</i>	20	<i>Pastinaca sativa</i>	352
<i>Gentiana amarella</i>	21	<i>Lotus corniculatus</i>	475
<i>Linum catharticum</i>	31	<i>Poterium sanguisorba</i>	764
<i>Cephalanthera pallens</i>	58	<i>Scabiosa columbaria</i>	785
<i>Chlora perfoliata</i>	80	<i>Ononis spinosa</i>	796
<i>Carlina vulgaris</i>	98	<i>Onobrychis sativa</i>	1005
<i>Daucus carota</i>	100	<i>Verbascum thapsus</i>	1018
<i>Fragaria vesca</i>	135	<i>Thymus serpyllum</i>	1054
<i>Bromus erectus</i>	151	<i>Silene inflata</i>	1099
<i>Anthyllis vulneraria</i>	226	<i>Hypericum perforatum</i>	1277
<i>Hippocrepis comosa</i>	237	<i>Helianthemum chamaecistus</i>	1508

comparison. It must however be noted that the plants vary very considerably in the degree of thoroughness with which a unit volume of soil is exploited; thus, while the root system of *Bromus erectus* occupies a smaller volume of soil than does that of *Anthyllis vulneraria*, it is in much more intimate contact with that soil by reason of the very rich development of its roots. It is obvious that there is a very great variation in the volume of the soil exploited by the different species.

It will be observed that the bulk of the species under consideration have their chief feeding roots within 9 in. of the surface (see p. 90), that is approximately in the zone of which the water content was found to vary between

35.6 per cent. and 11.5 per cent.—a total range of 24 per cent. With the single exception of *Ajuga chamaepitys*, in none of the plants examined was it found to be the rule for the system to be entirely confined to the top 3 in. of soil, where the total range of variation of water content is 52.7 per cent.—a range more than twice as great as that found at 6–9 in.

The data obtained for the water contents at a depth of 27–30 in. show that the root systems of the more deeply rooting perennials, of which *Poterium* may be taken as a type, experience a range of water content of only 19.6 per cent. (with a minimum of 15.3) in the region in which the bulk of their roots occur.

One of the most striking characteristics of the more deeply rooted perennials is the extraordinary wealth of rootlets which may be produced in the natural interstices of the chalk rock.

When large blocks of chalk are levered out from the face of a fresh cutting at a depth of 2 ft. or more, a flattened and luxuriant network of roots is revealed lying in the plane of the crevice.

It is a generally accepted statement that roots develop in a given direction as a response to localisation of water supply, and indeed Weaver (1919) in his summary of *The Ecological Relations of Roots* concludes that root systems may be taken as indications of the distribution of soil moisture. It is possible that this localisation of roots in the crevices of the chalk may be correlated with questions of water supply, since these interstices may be saturated with water vapour, and indeed Sir G. Evans (1885) considers them to be important waterways in the chalk; or the problem may be a merely mechanical one, although this seems unlikely since most, if not all, of these roots do on occasion penetrate the solid rock. Whatever the explanation may be, the presence of the roots in these localised situations is significant; and they are sometimes so plentiful that the end products of their respiratory activity cannot but have an effect upon the surrounding chalk.

If each succeeding generation of roots tends to follow in the paths of its ancestors a leaching effect far from negligible must be produced, and such a suggestion inevitably leads to a discussion of the clay pockets which are a common phenomenon of chalk districts, particularly where the lower and middle chalk reach the surface.

During the course of the present investigations it was remarked that sections of small pockets always showed them to be in possession of a well-developed root system and frequently one belonging to a woody plant. It was also observed that there was frequently a tendency for the roots of plants in the chalk immediately adjacent to the pocket, to develop towards the edge of the pocket rather than in other directions—(*Silene inflata*, *Tussilago farfara*), this being doubtless a hydrotropism, since it has already been shown that the clay pocket tends to be moister than the surrounding chalk.

It has so often happened that clay pockets were found to occur where

there were patches of thorn scrub or groups of trees established on stretches of chalk that a correlation between the two has been insistently suggested. It may be mere coincidence, or it may be that the presence of clay favours the development of woody species either directly or indirectly; the evidence is as yet insufficient to determine—but, considered in conjunction with the marked localisation of the roots of some of the herbaceous perennials in the chalk fissures, and the leaching effects excited by the by-products of their metabolism, it seems probable that the underground systems of such plants play an important rôle in the initiation of clay pockets.

(b) LEACHING.

In a previous paragraph (see p. 87) it has been deduced that the leached surface soil of the down has accumulated *in situ*, and the depth to which such leaching has occurred is important both directly and indirectly (since it affects water content, etc.) in determining the depth of penetration of the root systems, as well as influencing the actual species present in the flora.

Another factor which is important in this connection is the rapidity of the transition from leached to unleached soil. On many stretches of downland there is a very gradual transition from the leached soil at the surface to the pure chalk rock below, but occasionally there is scarcely any transition stage and the line of demarcation is strikingly clear cut. This condition of abrupt transition occurs on one of the areas (Farthing Down) which came under the writer's observation, and which is referred to above in connection with water contents; here the leached soil was separated from the chalk below by a layer of flints some 2 in. thick and extending over several square miles. This flint bed seems to have been effective in retarding leaching below, and it is noteworthy that in this area there occur very few plants with deep root systems, and the frequency of those which do occur is very low compared with other chalk grass lands in the vicinity. Most of the species which are abundant on this down tend to have roots chiefly in the first 4 or 5 in. of soil. Thus *Filipendula hexapetala* (*Spirea filipendula*) and *Plantago media* are much more frequent here than elsewhere in the neighbourhood, and although a few deep rooters such as *Poterium sanguisorba* do occur they are much less frequent than in other local downland areas, and, in the case of *Poterium* at least, are less prolific in flowering and fruiting than elsewhere.

(c) DISTRIBUTION OF ROOT HAIRS AND MYCORRHIZA.

In the descriptions of individual root systems above, mention was made of root hairs, and fungal hyphae associated with the roots were also recorded. It was found that neither of these features could be satisfactorily observed on roots which had been washed only with water, since the soil particles were often so closely adherent that all attempts to remove them with a soft brush only resulted in damage to the root hairs. It was found that after washing,

immersion for a few seconds in a 5 per cent. solution of HCl loosened the soil particles and after rinsing gave a clean root with unbroken root hairs. Fungi were widespread and often abundant; but the investigation being in the nature of a preliminary survey, the nature of the association was not established in each case when fungi were observed, and it may frequently have been pathological.

In a few instances, however, as in *Chlora perfoliata*, *Polygala vulgaris* and *Linum catharticum*, very definite zones of mycorrhiza were observed and in *Chlora* such zones coincided with patches of derelict root hairs. Fungi were less usually associated with the more deeply rooted perennials than with the shallow types.

Root hairs showed a wide range of variation in their general distribution and numerical frequency; in some plants no hairs were seen (*Anemone pulsatilla*, *Helianthemum chamaecistus* and *Filipendula hexapetala*) such plants usually having roots with a corky covering; in some plants (*Carlina vulgaris*) only very few hairs were seen; in others the hairs are more frequent and may be scattered over the entire root system, as in *Chlora*, where they occur densely in local patches, or in *Linum*, where they are more evenly distributed. Whitaker (1923) has shown similar distributions in some herbaceous Compositae. In many plants the hairs are confined to the region just behind the tip (*Anthyllis vulneraria*, *Ononis spinosa*), while in some of the more deeply rooted perennials, such as *Poterium sanguisorba* and *Thymus serpyllum*, hairs are richly developed on the tip region of the lower roots lying in the chalk fissures, but they do not long persist, and where laterals occur in the surface soil the hairs are few in number and have a scattered distribution. The seedlings of these two last-mentioned plants, whose roots are confined to the surface soil, also have irregularly scattered hairs.

In one or more instances, e.g. *Cirsium acaule* and *Polygala vulgaris*, roots examined on one occasion were found to be almost destitute of hairs, while plants collected at another time showed hairs to be quite well developed. This suggests a seasonal variation, in which case such plants as *Filipendula hexapetala* and *Anemone pulsatilla*, on which no root hairs were seen, may produce ephemeral ones. The question requires further elucidation.

Snow (1905) has pointed out that factors reducing the rate of growth of a root may bring about an increase in the development of root hairs, and in this connection we may note that hairs are abundantly produced on some of the tips of the more deeply situated roots, which may frequently find difficulty in maintaining their potential rate of growth when in the chalk rock.

Snow has also shown that air saturated with water vapour tends to suppression of root hairs, and in this connection it must be noted that *Polygala* from wet clay had very many fewer hairs than individuals from the chalk, while in shingle hairs were still more richly developed, but factors other than water content were obviously involved here.

Several chalk plants were grown with their root systems in water for a period of 6 weeks, and, while this prevented the development of any new hairs on either *Taxus baccata* or *Helianthemum chaemacistus*, it had precisely the opposite effect on *Anthyllis vulneraria* and *Gentiana amarella*, both of which grew new roots which were densely covered with long hairs. Young plants of *Poterium sanguisorba* treated in the same way produced a few scattered hairs on the new roots developed in the lower part of the system, and on those near the surface of the water many short thick ones. It is therefore obvious that water may have an effect on the distribution of root hairs which varies with the species.

The root hairs of different species were found to vary considerably in length and width, and also in the thickness of the wall. The hairs of *Taxus baccata* were very curiously thickened with a sculptured and cuticularised wall.

(d) RELATION OF ROOT SURFACE TO LEAF SURFACE.

In a few species the relation between the maximum absorbing area and the transpiring area was worked out for purposes of comparison between the species, should it be found that there was any degree of constancy for a given species. The plants were examined from this point of view while they were in a more or less stable condition; that is, during the period of winter rest, and the results obtained would seem to point to a certain relationship between the areas of these surfaces being maintained while the plant is at such a stage.

Table VII. *Compared Areas of Root and Leaf Surfaces.*

	No. of specimens	Average ratio $\frac{\text{leaf area}}{\text{root area}}$	Range of variation
<i>Ophrys apifera</i>	15	1.1	2.2-0.4
<i>Polygala vulgaris</i>	6	2.3	3.4-1.6
<i>Chlora perfoliata</i>	6	1.3	1.5-1.0
<i>Linum catharticum</i>	2	9.5	10.2-8.8
Average for four species	—	3.5	—

The accompanying Table VII shows the results, which were particularly satisfactory in the case of *Ophrys apifera*, where for 15 plants examined the range of values obtained for the ratio $\frac{\text{leaf area}}{\text{root area}}$ was only 1.8. Two of the plants gave distinctly aberrant results; one of these was very poorly developed and carried only a single leaf, while the other seemed even more unique, as it gave a value 0.8 above that obtained for any of the other plants, but it did not appear to the eye to differ appreciably from the other specimens. If these two aberrant plants are disregarded, the average value remains the same but the range of values is only 0.5, which indicates a somewhat remarkable uniformity. Since *Ophrys* only has stomates on the lower side, that leaf surface was alone considered.

In the case of *Polygala vulgaris* only six plants were measured, but there was a wider divergence here, the specimens tending to fall into two groups,

one with a value of 1.6 and the other with a value of 2.8. In these young seedlings it was not found possible to state definitely whether the plants were *P. vulgaris* or *P. calcarea*, and, although they were all probably the former, it is just possible that the lower value represents one species and the higher the other.

Chlora perfoliata gave results closely approximating to those obtained for *Ophrys*, but *Linum catharticum* gave values differing widely from these.

None of these four plants has roots which normally develop cork layers when growing in the chalk, and it was therefore considered that the respective absorbing and transpiring areas could be approximately compared. It is not intended to suggest that the areas in question are equally active throughout, but it was considered worth while to show that in these cases and especially in *Ophrys* there tends to be a more or less constant relationship during the period of winter rest between the root area and the leaf area.

IV. PERIOD OF FOLIATION

A record of the seasonal activities of some of the plants of the chalk down has been made in order to determine whether such data would elucidate any of the problems of the water economy of the flora. Considering the xerophytic conditions of the environment, it would appear that a large proportion of the chalk grass-land plants maintain actively transpiring leaf areas well on into what is usually the hottest and driest part of the summer; and indeed it is remarkable in view of the fact that the chalk is a "warm" soil that the flora tends to reach its climax so late in the season.

The life histories of the plants under discussion fall naturally into several groups when classified according to the duration of their vegetative activity.

Group I. The spring-germinating annuals—a comparatively small group.

Group II. The winter annuals and biennials.

Group III. The perennials, of which some

(a) retain green leaves all the year round;

(b) have a rest period without leaves, July to September;

(c) have a rest period without leaves, October to March.

The accompanying Table VIII shows the classification of some of the chief plants, a few of which are selected for descriptive purposes below.

Gentiana amarella. Annual.

Seedlings appear during March and by July they reach a height of some 3 in., or, if the season is wet as in 1924, they may attain nearly twice this height. Flowering reaches its zenith by the first half of August, by which time the radical leaves have died off. The whole plant dries up early in September, the skeleton being much more resistant to disintegration processes than that of most of the plants considered.

Chlora perfoliata. Winter annual.

The seedlings appear in September and remain in rosette form until the

axis elongates in May, the old leaves then gradually withering. The flowers open at the end of June, but flowering specimens may be found well into October; these have arisen from seedlings which come up in the early spring.

Anthyllis vulneraria. Perennial.

Seedlings appear in August, by the end of which month a new crown of leaves is beginning to be developed on the older plants; these (20-30 in number) continue to grow until October and activity is then suspended until the end of April, when some more leaves are added before the semi-erect axis begins to elongate. Growth increases during the latter half of May and the flowers open early in June. The first seeds are shed about a month later when the foliage begins to wither. In 1924 this occurred before the seeds from the later flowers had matured.

Table VIII. *Period of Foliation.*

(Group I. Spring annuals:

**Ajuga chamaepitys*, *Carlina vulgaris*, **Chlora perfoliata*, *Euphrasia nemorosa*, **Gentiana amarella*, **Linum catharticum*, *Vicia sativa*.

* These may also occur as winter annuals.

(Group II. Winter annuals and biennials:

Chlora perfoliata, *Daucus carota*, *Echium vulgare*, *Erythraea centaurium*, *Inula conyza*, *Linum catharticum*, *Pastinaca sativa*, *Reseda luteola*, *Teucrium botrys*, *Verbascum thapsus*.

(Group III. Perennials. (a) Active throughout:

Asperula cynanchica, *Astragalus danicus*, *Avena pubescens*, *Bellis perennis*, *Briza media*, *Bromus erectus*, *Cirsium acaule*, *Fragaria vesca*, *Hieracium pilosella*, **Helianthemum chamaecistus*, **Hippocrepis comosa*, **Lotus corniculatus*, *Medicago lupulina*, *Onobrychis sativa*, *Plantago lanceolata*, *Plantago media*, *Polygala vulgaris*, *P. calcarea*, *Poterium sanguisorba*, *Filipendula hexapetala*, **Thymus serpyllum*.

* These tend to lose their leaves in hard winters.

(b) Summer rest, *cir.* July-Sept.:

Anthyllis vulneraria, *Gymnadenia conopsea*, *Ophrys apifera*, *Orchis maculata*, *Viola hirta*.
Onobrychis sativa and *Asperula cynanchica* are sometimes to be included in this group.

(c) Winter rest, *cir.* Oct.-Mar.:

Anemone pulsatilla, *Brachypodium pinnatum*, *Centaurea scabiosa*, *Cichorium intybus*, *Convolvulus arvensis*, *Galium verum*, *Hypericum perforatum*, *Ononis spinosa*, *Origanum vulgare*, *Phyteuma orbiculare*, *Primula veris*, *Prunella vulgaris*, *Reseda luteola*, *Scabiosa columbaria*, *Senecio jacobaea*, *Silene inflata*, *Tussilago farfara*.

Brachypodium pinnatum. Perennial.

New leaves are produced early in April, but it is not until the end of the month that these have grown sufficiently to push their way up through the old dead leaves. Flowering begins in mid-June and the leaves maintain their appearance of vegetative activity until November.

Ophrys apifera. Perennial.

Some young plants, apparently seedlings, were found early in October and these had only two leaves until mid-March. Normally the young axes arise in late August from the new tubers of the parent plant and by the end of September these bear a rosette of 3 or 4 leaves, growth then ceases until early March when another leaf may unfold but no further development occurs until early May when the axis begins to show and then to elongate. This activity is some 3 weeks after growth has been renewed by the bulk of the surrounding

plants, and the plants of *Ophrys* are therefore less conspicuous than during the early part of the year. Flowering occurs in the second half of June, by which time the old basal rosette of foliage leaves has withered; the other aerial parts dry up, the cauline leaves being shed as the capsule ripens and sheds its seeds towards the end of July.

Polygala vulgaris.

Both this and *P. calcarea* are biennials though they often survive for a third season. Seedlings may be found in August and are well developed by the end of September, when they may easily be distinguished from the old plants by their more upright habit. The primary axis is prominent, bearing at its summit 4 or 5 young branches. In plants of the previous year the habit is straggling, leaves being chiefly confined to stems of that season's growth. Flowering begins in the middle of May on the old plants and rather later on the young ones; the foliage leaves are mostly shed and the seeds ripen in June; there is a short rest period and new vegetative growth takes place on the young plants in July and August.

Poterium sanguisorba. Perennial.

Seedlings germinate in early September and the young plants pass the winter with 3 or 4 leaves. They do not flower during the following year. Older plants produce a new crown of leaves about the same time as the seedlings appear, or rather earlier, and maintain these throughout the winter. New leaves may be added as early as January if the weather is favourable, and subsequently those added increase in size, the flowering axes form and begin to elongate in mid-May, flowering beginning in early June and continuing on into August, the old leaves gradually dying off as they are replaced by young ones. Vegetative activity is maintained in this plant as long and as vigorously as in any other plant of the habitat and considerably more than most, a feature which suggests a correlation with the deep and efficient root systems (but cf. *H. pilosella* with shallow roots).

Ononis spinosa. Perennial.

This plant passes the winter well below the surface of the ground and no traces of it can be seen for rather more than 6 months. Flowering usually begins at the very end of June and continues into September, the foliage being well maintained throughout—and this plant is therefore active vegetatively during what is generally the driest season on the chalk down, and may be regarded as a most successful xerophyte. The plant begins to dry up in September and disintegrates very rapidly in the early autumn rains; it may in fact be impossible to locate during the first week in October.

Considering the constitution of the chalk grass-land flora, the paucity of ephemerals is seen to be one of its most striking characteristics, this being doubtless due to the usual denseness of the turf, which forms a closed community. Species such as *Anagallis arvensis*, *Stellaria media*, *Myosotis collina*, *Senecio vulgaris*, etc., may occur where the surface has been disturbed by

rabbits, but these plants are not strictly members of the grass-land community.

Of the plants most characteristic of the habitat the greater number retain their vegetative parts above ground throughout the winter months, this group including both shallow and deeply rooting species.

All of the more deeply rooting perennials are either summer green or evergreen, though *Onobrychis sativa* may sometimes have a summer rest period, and all the plants which winter below the surface of the ground belong also to this group. A few plants such as *Galium verum* may begin their inactive period as early as August if fruiting is not delayed, but they are best considered as plants with a winter rest since they do not become active again until the following spring.

Of the more shallow-rooted species several are evergreen (e.g. *Bromus erectus*, *Polygala* spp.), but a number have a period of summer rest. In view of the fact that the mean water content of the surface in summer is but little more than half that during the winter months and may fall below 9 per cent. the summer rest exhibited by such characteristic species as *Ophrys apifera* and *Anthyllis vulneraria* is not surprising.

V. DISTRIBUTION OF STOMATES.

With a view to comparing the different species of the habitat in relation to the number of stomates present per unit area, a survey was made during the last week of May and the first week of June, and in each species the last-formed mature leaves were used for examination. The accompanying table shows the average values obtained for the leaves of each species.

It will be seen (Table IX) that most (77 per cent.) of the typical herbs of the chalk down have stomates on the upper as well as on the lower surfaces of their leaves; in fact several (23 per cent.) have a larger number above than below, these include four members of the Leguminosae (*Anthyllis*, *Lotus corniculatus*, *Lathyrus nissolia* and *Onobrychis*, also a very characteristic chalk plant, *Linum catharticum*).

The leaves of both the woody species examined (*Rhamnus* and *Cornus*) are well supplied with stomates but these occur on the lower surface only. The total number of stomates present do not place these shrubs in a category apart from the herbaceous plants.

It is noteworthy that in plants of both *Chlora* and *Polygala* from wet clay fewer stomates were present than in similar plants growing on chalk.

Several species (e.g. *Anthyllis*) comparatively well supplied with stomates were seen to be among those plants with a period of summer rest; but it is by no means the rule for plants with such a rhythm to have many stomates, since, for example, *Ophrys* has fewer stomates than most of the other plants considered.

No definite relation could be found to exist between the number of stomates and the extent of the root system.

Table IX. *Number of Stomates per 1 sq. mm. Leaf.*

Species	Lower surface	Upper surface	Total
<i>Plantago lanceolata</i>	225	267	492
<i>Thymus serpyllum</i>	366	88	454
<i>Plantago media</i>	254	184	438
<i>Onobrychis sativa</i>	135	248	383
<i>Sonchus arvensis</i>	374	4	378
<i>Helianthemum chamaecistus</i>	328	44.4	373
<i>Verbena officinalis</i>	273	67	340
<i>Origanum vulgare</i>	311	28	339
<i>Cornus sanguinea</i>	333	0	333
<i>Centaurea scabiosa</i>	130	185	315
<i>Polygala vulgaris</i> (chalk)	160	142	302
<i>Reseda luteola</i>	180	122	302
<i>Daucus carota</i>	225	39	264
<i>Hieracium pilosella</i>	148	115	263
<i>Anthyllis vulneraria</i>	105	155	260
<i>Viola hirta</i>	201	56	257
<i>Polygala vulgaris</i> (shingle)	161	96	257
<i>Lotus corniculatus</i>	93	155	248
<i>Rhamnus catharticus</i>	248	0	248
<i>Linum catharticum</i>	109	129	238
<i>Hypericum perforatum</i>	233	0	233
<i>Fragaria vesca</i>	223	0	223
<i>Polygala vulgaris</i> (clay)	120	91	211
<i>Lathyrus nissolia</i>	29	176	205
<i>Inula conyza</i>	104	94	198
<i>Silene inflata</i>	93	100	193
<i>Vicia cracca</i>	191	0	191
<i>Ranunculus bulbosus</i>	151	35	186
<i>Verbascum thapsus</i>	166	10	176
<i>Geum urbanum</i>	175	0	175
<i>Silene inflata</i> (var. <i>puberula</i>)	121	49	170
<i>Ononis spinosa</i>	91	76	167
<i>Gentiana amarella</i>	127	32	159
<i>Viola canina</i>	141	0	141
<i>Ophrys apifera</i>	81	0	81
<i>Chlora perfoliata</i> (chalk)	61	12	73
<i>Chlora perfoliata</i> (clay)	34	18	52

VI. WILTING

The wilting point was determined for a few of the chalk-down species, but since the method employed had distinct limitations the plants considered were only the more shallow-rooted types. The root systems of such plants have in nature greater extremes of water content to endure than those which are more deeply rooted, and they were therefore of particular interest as the subjects of wilting experiments.

Blocks of soil some 6 in. or more in diameter and of rather greater depth were removed with the plants *in situ* and without disturbing their root systems; and after having the freshly cut soil surfaces protected from loss of moisture by several layers of grease-proof paper, the experimental blocks were transferred in flower pots to the shelter of a glass verandah. Here they were exposed to the ordinary variations of climate but received no supply of water either from rain or by means of capillary forces. In a few control experiments plants were wilted off rather more quickly by taking them into a greenhouse.

The method affords an indication of the ability of the plants concerned to withstand lack of water in the substratum, and possibly a rough basis for comparison between different species. A considerable range of values was obtained for the water content at the wilting point but it was found that the variations could be correlated with environmental factors to a great extent.

Of prime importance was the rate at which the process of wilting took place, and, as would be expected, the longer the plants took to succumb the lower was the wilting point, because the plant had a longer period in which to perfect its readjustment.

In nature capillary movement of water (see p. 81) would have an important effect in slowing down the wilting process, thus giving time for a fuller adjustment on the part of the plant and thus rendering available a higher percentage of soil water than would otherwise be the case.

Table X. *Wilting Coefficients.*

The figures given represent the water content at the wilting point, and are generally the averages obtained for duplicate specimens.

Duration of experiment ...	Days				
	15-20	35-40	35-45	70-101	101-115
	I	II	III	IV	V
<i>Anthyllis vulneraria</i>	9.99	—	5.07	—	—
<i>Bellis perennis</i>	—	—	7.64	—	—
<i>Brachypodium pinnatum</i>	10.52	—	—	—	—
<i>Chlora perfoliata</i> (seedlings)	12.67	—	5.85	5.61	—
(adult)	—	—	10.98	—	—
<i>Daucus carota</i>	5.93	—	—	—	—
<i>Erythraea centaurium</i>	12.60	—	5.41	—	—
<i>Festuca</i> sp.	10.25	—	—	—	—
<i>Fragaria vesca</i>	10.52	—	—	5.27	4.16
<i>Hieracium pilosella</i>	10.04	—	—	4.17	3.90
<i>Inula conyza</i>	—	4.98	—	—	—
<i>Ophrys apifera</i>	10.27	5.50	4.91	4.42	3.21
<i>Origanum vulgare</i>	11.03	—	—	—	—
<i>Plantago lanceolata</i>	10.25	—	—	—	—
<i>Polygala vulgaris</i>	—	6.43	—	5.31	—
<i>Poterium</i> (seedling)	10.02	—	7.64	—	—
<i>Viola hirta</i>	—	—	7.53	—	—

Several of the plants showed an incipient wilting effect some 3 or 4 days after the beginning of the experiment (this was especially marked in *Chlora* and to a lesser degree in *Ophrys*), thus marking a period during which the plant experienced a deficiency in water supply, but had as yet been unable to complete its adaptations to the new conditions of the environment; the process of adjustment having ensued, the aerial organs of the plant then resumed their more normal appearance after the lapse of about a day. It was mostly the younger leaves which exhibited incipient wilting, but when eventually permanent wilting set in, it was the older leaves which suffered first (as shown particularly by *Ophrys*).

The lowest wilting point values were obtained for a set of plants cut out from the chalk down in mid-November, most of which wilted only towards the end of February, a period of approximately a hundred days. This set of

plants wilted more slowly than any other; they were subjected to a spell of severe frost during the latter part of the time but they appeared to be quite unaffected, though most of the seedlings of *Chlora* and a few plants of *Ophrys* on the downs were badly frost-bitten. The lower water content must have been a considerable advantage.

To a certain extent variation in wilting point could be correlated with the season of the year, but since weather conditions in turn influence the rate at which wilting takes place, observed seasonal variations must be regarded as secondary. Thus, in winter and early spring the water content could fall much lower before permanent wilting set in than was found to be the case in September and October when the weather was warmer and drier. Age was also found to be an important factor: for an old flowering plant of *Chlora*, already almost at the end of its life cycle, was found to be less resistant than a young seedling of the same species, and in general the older leaves on a plant wilted before the younger ones.

Some of the experimental blocks of soil were set aside, and when all the plants were apparently quite dead, the soil was watered and kept moist. In less than 3 weeks it was found that both *Ophrys* and *Fragaria* were producing new leaves, although none of the other plants (*Festuca* sp., *Bellis perennis*, *Linum*, *Polygala*, *Poterium* seedling) showed any sign of life.

Examination showed that in *Ophrys* all the roots had become black and disintegrated, and, while no new roots had as yet been formed, the tuber with the young one developing alongside it remained healthy in appearance. In *Fragaria* the old roots were present, but they were soft and discoloured, and were possibly not functioning; there were three young roots about half an inch long on the younger part of the rhizome. It is thus obvious that these two plants are able to withstand very severe drought conditions (the water content of the soil around their roots was most probably less than 2 per cent. before water was given), and it was doubtless the tuber in the one case, and the well-developed rhizome in the other, which enabled the plants to survive. In the case of *Fragaria* the collapse of the aerial organs was presumably due to the breakdown of the translocation mechanism within the plant itself, or its failure to meet the demands made upon it, since the rhizome was enabled to survive. It is perhaps by virtue of the limitations of the organisation of the translocating system that the water content of the rhizome remains above the lethal point.

On the chalk down the lowest natural water content recorded for the surface 3 in. was 8.58 per cent. during the early summer drought of 1925, at which time none of the plants observed seemed to be adversely affected; yet of the plants tested for wilting point in October, 13 out of 14 of the species had wilted before the soil-water content had sunk to this value. But it must be remembered that while in the case of the experimental plants the water-content value was more or less constant throughout the block of soil, in nature

there would be an increasingly greater water content downwards from the actual surface, and thus a steady if meagre supply of water to the roots, particularly to the lower ones, which would allow for a slow and steady readjustment on the part of the plant (see above for effect of capillarity)—so increasing its drought-resisting capacity. We thus find that when the minimum water content for the surface 3 in. was 8.58 per cent. that for the top 9 in. was 10.04 per cent., a value at which several of the plants under experiment had already wilted, when the process was comparatively rapid. When the process was slowed down there was a tendency for the plants to reach the wilting point when the water content was about 5 per cent. Compared with conditions existing in nature, this would leave a balance of some 3.5 per cent. water available when the drought period was at its height. But it must be borne in mind that under exceptional conditions the wilting coefficient may rise above 10 per cent. for a large number of species. In view of the results obtained it would seem that in nature the surface-water content is insignificant compared with the water content of the soil below, which in the chalk rises rapidly with increasing depth. We thus have a supply of water from below the surface levels which enables the plants to readjust their osmotics to drought conditions, and capillarity therefore appears to be an important factor in slowing down the wilting time and rendering available a higher percentage of water. It is thus that the plants of the chalk down may be enabled to survive drought conditions.

VII. SUMMARY

1. A record of the seasonal and spatial variations in water content for a given area of chalk down was kept from January 1924 to August 1925, this including periods of both drought and excessive wet. Readings were taken at four successive depths in the region chiefly exploited by the roots of the herbaceous species, i.e. from the surface to 2 ft. 6 in. (76 cm.) It was shown that although high water contents might be recorded, and the average value of the water content was comparable to that of mesophytic communities, very low minimal values occurred, especially at the surface, where there was a wide range of fluctuation in the water content.

2. The importance of evaporation as a factor influencing surface-water content was shown to be considerable both during the winter and summer months, whilst the effect of dew deposition, though slight, would appear not to be negligible.

3. It is considered that capillary action may be of importance in chalk soils in dry periods. The water content at 2 ft. 6 in. never fell below 15 per cent., and increases in its value at this level occurred at times when percolation could not be regarded as an important factor.

4. The minimum water content recorded for the surface of the down was 8.58 per cent. and the surface maximum 61.29 per cent., but for other chalk

grass-land areas with a more leached surface values up to 98·4 per cent. were recorded.

5. A variety of species was examined with a view to determining the non-available water in the soil by allowing them to wilt slowly. The rate at which the process occurred was shown to be of great importance; and although plants with possibilities of subterranean reserve water supplies (e.g. *Ophrys* and *Fragaria*) were able to survive, even after both shoot and root had withered, the majority of species, even under favourable conditions (i.e. a very slow wilting process) failed to use the last 5 per cent. of water present. It would therefore appear, from the results obtained, that the available water in chalk soils during a period of summer drought may fall to about 3·5 per cent., although the average available water content at the surface for the period of drought (about 6 weeks) was approximately 8 per cent. It was also shown that under certain conditions a water content of over 10 per cent. may be insufficient to support the life of plants.

6. At the surface the lag between precipitation and rise in water content was inconsiderable, but at a depth of 2 ft. 6 in. the lag may amount to a week.

7. The steeper slopes of the down were shown to have a lower water content than the crest.

8. Bare ground was shown to be drier than that with a covering of vegetation.

9. The water content, though not agreeing closely with the varying spatial values of any of the soil constituents, showed the most marked relation to the organic content; the factors deduced for the water-holding capacity of the respective soil fractions being approximately in the following ratios: CaCO_3 0·2, "clay" 0·6, organic 1·75.

10. Some records were made of the air content of the upper parts of the chalk soil, and it was shown that chalk soils are well aerated in comparison with other types of natural soil in this country.

11. A number of root systems were examined and a wide variation of type was found to occur. Considering some fifty characteristic species, the average extent of the working depths of the root systems was 4–8 in., while the mean maximum penetration was 12·1 in. The most deeply-rooted species of the chalk-down flora were found to include *Ononis spinosa* and *Poterium sanguisorba*, both of which may possess root systems extending to a depth of 3 ft. The plants were divided into three classes according to the depth of penetration of their root systems.

12. The soil at a depth of 6–9 in. frequently proved to be more moist than at a lower level, while soil aeration decreases with depth. It would therefore appear that the combined optimum for aeration, water content and minimal fluctuation of the latter, occurs at a level between 6 and 9 in. from the surface. It is significant that the average working depth of the root systems of characteristic species coincides closely with this zone.

13. The most widely divergent types of root system were found among the more shallow-rooted species, i.e. those with roots confined to the first 6 in. of soil; among these both fleshy and fibrous systems were found, as well as many varieties of form.

14. The second group of plants with roots extending to a depth of 15 in. showed the widest range of variation of root from within the species, and this was considered to bear some relation to the fact that these roots are chiefly developed in the region of the soil where transition to the solid rock takes place, the nature and depth of this zone being very variable. Several members of the Leguminosae were conspicuous here, *Anthyllis vulneraria* being particularly variable.

15. The third group of plants, those with roots more than 15 in. deep, is chiefly remarkable for the rich development of roots in the fissures of the chalk; and it is suggested that the CO_2 produced by their respiration may have an important leaching effect. These species have roots which penetrate to the level at which the capillary water supply is appreciable and are therefore least affected during periods of low precipitation.

16. Both the degree and extent of leaching may have an effect upon the root systems, since water content and other factors are involved. This is shown by comparison between the flora of Farthing Down and other chalk areas.

17. The distribution of mycorrhiza and root hairs is described and both are shown to be very variable. In only a few instances was mycorrhizal attack shown to occur in definite zones, but the great majority of species examined were found to have fungal hyphae associated with their root systems. While certain species were destitute of root hairs when examined, the roots of most species were found to be well furnished with hairs (especially among some of the deeper rooters), whilst some retain their root hairs for a considerable distance behind the root tip.

18. The relation of root surface to leaf surface was found to be remarkably constant in some species, e.g. *Ophrys apifera*.

19. The period of foliation is described for a number of species, and the small proportion of ephemerals which occur is remarked upon. Certain species have a period of summer rest occurring when drought conditions are apt to supervene.

20. A census of stomates was made in order to afford a basis for comparison. On the whole, the characteristic species of the chalk flora were found to be well supplied with stomates, while 77 per cent. of the 35 species examined had stomates on both upper and lower leaf surfaces.

The water-content data show that the surface 3 in. of soil furnishes the largest average water supply; whilst the averages for all the lower levels are of the same order of magnitude. The data respecting wilting coefficients indicates that, despite the marked differences in water content at the wilting

point according to the external conditions, the majority of the chalk plants are liable to suffer injury if the water content of the soil falls below 10 per cent. It is apparent, therefore, that the surface layer where the minimum may fall below 9 per cent. is incapable of supplying a sufficiency of moisture for the majority of the calcicole species during the summer months. On the other hand, there is little difference either as regards the means or minima between the 6 to 9 in. horizon and that from 12 to 15 in. The aeration data show that the air content decreases rapidly with the increase of depth and it may therefore be assumed that here as in woodlands (cf. Salisbury, E. J., *Structure of Woodlands*, p. 384) the rooting depth is a compromise between the adequacy of water supply and the inadequacy of aeration. From this point of view the subsurface would appear to afford the optimum compromise; and the data furnished respecting rooting depths show that, whilst a few characteristic species have deep root systems, the majority possess roots that penetrate to a depth of from 3 to 6 in.

Exceptions are furnished, *inter alia*, by *Hieracium pilosella* and *Ophrys apifera*, both of which have very shallow root systems but which were found to be capable of withstanding appreciably lower water contents than the other species experimented with.

The chalk flora has been generally accepted as a xerophytic community, and the present investigation confirms this estimate; for although during the greater part of the year there is a wide margin of water available in the soil for the use of the plants, in dry periods this may soon fall to the danger line. It is the ability of the species to weather these drought periods which in a community of perennials must determine the floristic composition. The roots of the covering vegetation lie within 3 ft. from the surface but the greatest root development is confined to the upper 9 in. and it is the movement of water in this zone which is of prime importance to the plant community. Doubtless this small margin of available water supply is largely responsible for the comparatively low average stature which the vegetation of the chalk down attains, and the even contour of its profile.

In conclusion I should like to express my thanks to Dr E. J. Salisbury, to whose continual help and advice any merit of this work is due, and to whom I am indebted for permission to publish Figs. 15, 18, 20 and 25.

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STUDIES ON THE VEGETATION OF NOTTINGHAMSHIRE¹

I. THE ECOLOGY OF THE BUNTER SANDSTONE

BY J. W. HOPKINSON

(With Plate I, a Folding Map and two Figures in the Text.)

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INTRODUCTION

Up to the present, the plant communities of the Bunter Sandstone of Nottinghamshire have escaped the attention of British ecologists, and have

¹ The greater portion of this paper formed the subject of a Thesis accepted by the University of London for the degree of M.Sc.

gone unrecorded, except for a few brief references to dry oakwood and oak-birch-heath in *Types of British Vegetation* (19) and "The Woodlands of England" (13). In the *Victoria County History of Nottinghamshire*, Prof. Carr (5) describes the general geological distribution of the flora, including the Bryophyta. Although the county possesses the finest primeval oakwoods in Britain, it is a melancholy fact that "the published botanical literature of Notts., since the time of Howitt (1839)... is very scanty" (5, p. 43). The presence of *Quercetum sessiliflorae* is of itself sufficient to make its ecological study interesting, in view of the progress made in our knowledge of that plant consociation, by the researches of Moss (12), and more recently of Salisbury and Tansley (15). The purpose of the present paper is to give a general account of the Bunter vegetation.

GEOLOGICAL STRUCTURE (Fig. 1, p. 133)

The area concerned in this investigation may be described as west-central Nottinghamshire, and extends approximately from Nottingham to the River Meden, a distance of 20 miles (32 km.). The county is essentially lowland in character. Only one fifty-sixth of its surface lies above 600 ft. o.d. and this high ground includes the Robin Hood Hills and much of the Bunter escarpment on the west. The bulk of the southern part of the outcrop lies above the 200 ft. contour. Further north the Bunter produces some of the lowest ground in the county, where the soft sandstone has been easily denuded in the neighbourhood of the river valleys.

THE BUNTER SANDSTONE.

The outcrop of the Bunter has an area of 219 sq. miles and occupies about 26 per cent. of the surface of the county. The line of strike of the various geological formations runs from north to south. On the left side of the Trent, there are three prominent escarpments, the Permian, the Bunter, and that of the Keuper Waterstones. The outcrop of the sandstone is therefore well defined, and from the top of the escarpment, at 600 ft. o.d., the rock, with a broad eastern slope, dips to the base of the Waterstones at about 150 ft. o.d. The Bunter is about two miles wide near Nottingham but it broadens out rapidly to the northward and maintains a width of from six to nine miles. Borings show that the series undergoes a gradual and progressive increase in thickness to the north and north-east, from 221 ft. at Ruddington to 564 ft. at South Scarle.

In the area surveyed, the Bunter Series is separable into two subdivisions, the Lower Mottled Sandstone below and the Pebble Beds or Conglomerate above.

The Lower Mottled Sandstone is a fine grained, soft sandstone, generally red in colour, but mottled with yellow and white, the mottling of lighter tints being due to the removal of the film of oxide of iron that surrounds the grains.

It shows marked current bedding, and there is a general absence of pebbles except to the west of Nottingham. Bands of clay are present, and in general there is more argillaceous material than is present in the Pebble Beds. From a thickness of 20–30 ft. near Nottingham, it increases northwards to 70 ft. in the Robin Hood Hills and to about 100 ft. at Mansfield. It has a narrow outcrop extending from Nottingham into South Yorkshire, with indefinite boundaries both above and below, for there is a perfectly conformable passage from the Permian Marl at the base, whilst above, “only occasionally does a distinct line of separation mark the slightly changed conditions of deposition” (16).

The Pebble Beds “are mainly composed of rather coarse sand with a somewhat sparse admixture of pebbles which sometimes occur isolated and sometimes in broken strings and clusters, but rarely in segregated masses” (10). “The prevalent tint of the sandy portion is pale yellow or buff, yet in the forest country it is a dull red, with the highest portion often nearly white” (16). “The sand is sufficiently compact to form a sandrock but . . . can be crumbled readily between the fingers” (10). “The general absence of a cementing material leaves the sandstone so soft and friable that it has never been of use as a building stone” (18). False bedding is well marked, as in the rock below. The sandstone is barren of fossils except in the pebbles. These are smooth and well-rounded stones, chiefly of quartzite derived from rocks of pre-Cambrian and older Palaeozoic ages. Boulders of clay are known also to be present.

SUPERFICIAL DEPOSITS.

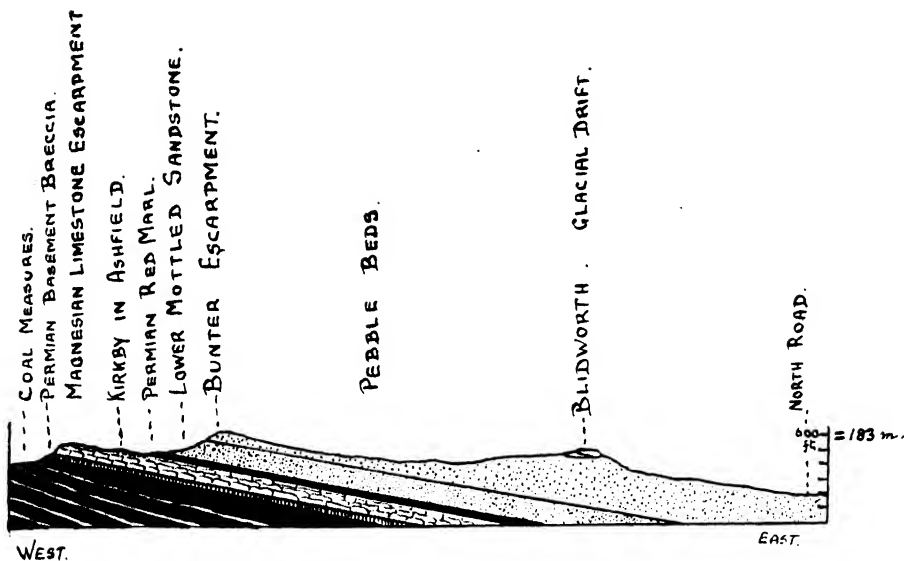
The glacial deposits of the Nottingham district occur chiefly as isolated patches of Boulder Clay, sand, and gravel. At Blidworth, on the Bunter, there is a mass of red Boulder Clay with abundant erratics, derived from igneous rocks of the Lake District, Millstone Grit, and Magnesian Limestone. These erratics are scattered sparingly over the country between Mansfield and Farnsfield.

Glacial gravels occur in Annesley Park 600 ft. above sea level, the material being partly loose and partly conglomeratic, derived mainly from the Bunter but also containing Jurassic limestone. Drift gravels cap some of the hills to the north but do not extend much beyond Mansfield Woodhouse, as near Worksop there is no trace of them.

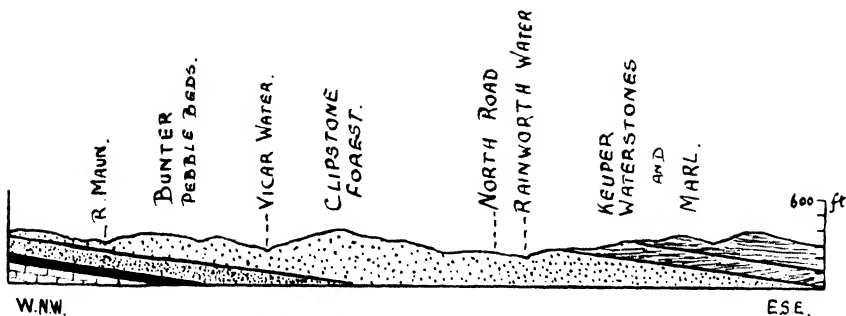
It will be seen, therefore, that the bulk of the drift has been removed by post-Glacial denudation, and the Glacial deposits have no serious influence on the vegetation of the Bunter Sandstone as a whole; although, in the discussion of plant habitats on the sandstone and the drift, certain considerations must be taken into account. For example:

(a) The gravels may consist entirely of detritus derived from the Bunter, and may therefore produce a similar habitat.

(b) The presence of clay in several places on the Bunter outcrop should



SECTION FROM KIRKBY-IN-ASHFIELD TO THE NORTH ROAD NEAR
FARNFIELD.



SECTION FROM THE R. MAUN TO NEAR BILSTHORPE, CROSSING CLIPSTONE

[BASED ON THE GEOL. SURVEY.]

FOREST.

0 1 2
MILES.

Fig. 1. Two geological sections from west to east across the Sherwood Forest area. The upper section passes across the southern part of the forest, where the Bunter escarpment is holdest and highest. The lower passes further to the north and shows the relation of the Bunter to the Keuper beds.

be noted; these areas are marked on the Geological Survey maps and are apparently unconnected with drift, but the gravels also may contain clay in sufficient quantities to affect the vegetation.

(c) The Drift may contain cementing material, as in the case of the conglomeratic deposits at Blidworth, Annesley Park, and hills to the north and east. The presence of a substratum of boulders just beneath the surface in the Drift at Ollerton has been noted, and its effects on the woodland vegetation will be described later.

Alluvium. On the Bunter, river gravels and alluvium are confined to the valleys of the few streams that cross the outcrop, e.g. the Maun, the Meden, and their tributaries. Except for a few brief references, the vegetation of these soils is not described in the present paper.

SCENERY

From the foregoing notes it will be gathered that the Bunter country is undulating in character, with hills that have a steep slope to the west and a gentle slope to the east. The absorbent capacity of the rock is high and there is very little surface drainage. A few streams rise in the high ground in the west of the county. Of these, the Leen and the Erewash flow southwards to the Trent along the outcrops of the Coal Measures and the Permian Marl respectively. The Maun, the Meden, and further north, the Poulter and the Ryton run eastwards across the Bunter outcrop and join the Idle, a left bank tributary of the Trent. These are the longest streams in the county, and it is only in their valleys and those of their tributaries that the water table reaches the surface, except on the eastern edge of the outcrop, "on low ground at its [the Bunter outcrop's] top where the easterly dip carries it beneath the impervious Keuper, and the pent-up waters escape, as it were, over the tilted lip" (10).

The rivers and streams do not depend immediately on the rainfall, are not transformed into torrents after falls of rain, and are seldom subject to floods. Lateral erosion keeps pace with vertical, and consequently they have wide valleys. "Instead of gorges, there exist on either side flats with marshes and marsh vegetation" (18).

"Nevertheless the Bunter country is everywhere characterised by ramifying valley systems, clearly the result of erosion by running waters at some bygone period, but now all, or nearly all, *permanently dry*" (10).

CLIMATIC CONDITIONS

In Nottinghamshire the prevalent winds are those from the south-west and west, and blow for one-third of the days in the year. Easterly winds are commonest in March, and give rise to the dust storms so frequently seen in the Bunter country at this time of the year.

Temperatures are relatively extreme, for there is an annual range of

39° F. (nearly 22° C.) between the average minimum in January of 31° F. (— 0·4° C.) and the average maximum in July, of 70° F. (21° C.), whilst a daily range of 26° F. (14·5° C.) has been recorded (May 20th, 1909). The amount of sunshine is moderate, the average for 25 years being 1252 hours (at Worksoy).

Rainfall. Maps by Col. Mellish (in Swinnerton, *County Geog.*) and H. R. Mill (in Goodwin, *Soils of Notts.*) show that the whole of the area, from Nottingham to the River Meden, has an average rainfall just exceeding 25 in. (635 mm.), but on the Bunter further north, where the ground is lower, the average falls below 25 in. (635 mm.). The rainfall is highest on the Robin Hood Hills where it reaches 30 in. (760 mm.), and there is quite an obvious relation between the distribution of the rainfall and the physical features of the county as a whole, the isohyetal lines running more or less parallel to the escarpments. In dry years the rainfall on the Bunter may be as little as 16 in. (408 mm.) as in 1921, and in wet years, as much as 36 in. (915 mm.) as in 1919, 1920. Seasonal records show that the summer rainfall is high, as about two-fifths of the total rain for the year falls from May to August inclusive.

EDAPHIC CONDITIONS

The soils of the Bunter are dry and sterile; mechanical analysis shows that they are composed of from 80 to 90 per cent. of coarse and fine sand, the former greatly predominating. The relatively small proportions of clay and humus give it lack of cohesion, and make it open and friable. In addition, the humus is frequently derived from xerophilous plants and is often undecomposed. For these reasons and owing to the dryness and the consequent paucity of earthworms and bacteria, the colloid content is extremely low, and hence the soil has very little power to adsorb and retain water and soluble salts. Drainage is excessive owing to the large size and roundness of the grains and the high degree of porosity of the sandstone below. The capillarity of the soil is slight, and it has little power of raising water. The depth of the water table is an important factor. On the Lower Mottled Sandstone and on the scarp slope generally, the seepage from higher ground is considerable, and besides this, the clay content of the soils here is rather above the average. During the sinking of the well at Kirkby Waterworks, in a valley near Noman's Hill Wood, the first onflow of water occurred at the bottom of the Bunter Pebble Beds, 46 ft. 8 in. (14·2 m.) below the surface (416 ft. o.d. = c. 127 m.), and it should be noted that much of the surrounding country reaches 600 ft. (c. 183 m.). The sterility of some of the arable land in this region is apparent, even to the casual observer, and corn only 6 in. (15 cm.) in height, overgrown by the far too abundant spurrey, is a sight not infrequent in dry seasons. In this area the usual four-year rotation is often prolonged to five or six years, sheep being fed on the grassland for two or more years. On the other hand, in the deeper valleys of the Maun and Meden, the presence of the rivers shows the water table to be relatively nearer the surface, and the arable land is more

fertile. The water table also reaches to within 20 ft. (c. 6.1 m.) of the surface along the eastern border of the outcrop. The general absence of villages on the Bunter, due in part to the impossibility of obtaining water from shallow wells, emphasises the great depth of the water table and the sterility of the soil. The sinking of deep wells has tended to lower the general level of the ground water, for a number of hollows and valleys formerly wet are now dry, except immediately after a period of excessive rainfall.

The lime content is low and the soil consequently tends to become sour, spurrey (*Sagina nodosa*), sheep sorrel (*Rumex acetosella*), and other "acid indicating" plants being abundant on cultivated ground. Estimations of the hydrogen ion concentration were made in a few cases in the field, using Allen and Hanbury's Compound Indicator and Gimmingham's gravitational water method (8). A large number of samples were tested with potassium thiocyanate (6), and the colour reactions compared with a scale of five standard tints. The numerical results are given elsewhere, but it may here be said, that in every case where the humus, soil, and subsoil were tested as above or with litmus, an acid reaction was obtained, and in most cases it was pronounced.

The relative absence of calcium salts may result in the lack of physiological balance in the nutrient substances of the soil. Comparison with the more fertile but extremely variable soils of the Keuper Marl reveals the smallness, in the case of the Bunter, of the ratio of calcium carbonate to the total solutes present (taken as "loss on solution").

Table I. (*Compiled from Goodwin's analyses.*)

	Keuper	Bunter
	%	%
Average CaCO ₃ content of surface soils	2.40	0.147
Average "loss on solution" of surface soils	6.40	1.73
	Ratio = 0.38	0.085
Average CaCO ₃ content of subsoils	5.76	0.22
Average "loss on solution" of subsoils	8.39	1.77
	Ratio = 0.69	0.13

It has already been mentioned that local bleaching of the sandrock is characteristic of the Bunter, and it will therefore be expected that leaching of the surface soils will be very pronounced. Decolorised sand grains are abundant in every sample examined, both of the soil and subsoil, and the surface of arable land, of grass heath, and of bare ground after fires is white with bleached sand, particularly after heavy rains. If the humus is carefully removed from woodland soil, or the peat from heaths, the surface is seen to have the same appearance. To compare in some measure the leaching of the Bunter soil with that of the richer Keuper Marl, the difference between the "loss on solution" of the soil and the subsoil may be considered, and also their general composition. In the case of the Bunter, the data are the averages of numerous analyses, but Keuper soils are extremely variable and the values given are based on the analysis of a single typical fertile soil.

Table II. *Comparison of Keuper and Bunter soils.*

		Keuper	Bunter
Clay content	Soil	3.66	0.27
	Subsoil	13.11	0.47
Loss on solution	Soil	5.96	1.73
	Subsoil	9.60	1.77
Loss on ignition	Soil	4.82	3.26
	Subsoil	4.23	2.34
Total potash (K_2O)	Soil	0.544	0.0445
	Subsoil	0.6936	0.0162
Total phos. acid (P_2O_5)	Soil	0.1242	0.1165
	Subsoil	0.1136	0.0753
Nitrogen	Soil	0.157	0.117
	Subsoil	0.0316	0.079
Lime as carbonate	Soil	3.76	0.1468
	Subsoil	8.24	0.220

Thus the loss on solution is greater in the case of the Marl, but certain facts must be set against this. The colloid content is greater in the Marl, particularly in the subsoil, and therefore the adsorption of NH_4 , K, and PO_4 ions is greater too. It will be seen that the K_2O content is greater in the subsoil than in the soil, the P_2O_5 content nearly as great, and *vice versa* in the case of the Bunter. In both soils there is a greater nitrogen content than in the subsoils, owing to loss of nitrates by solution in the drainage water.

Other factors influencing the composition of the surface soil are:

(1) *The "general insolubility of the soil constituents" (10).* Analyses of the ground waters of the Bunter, Keuper Marl, and Magnesian Limestone support this statement:

		Total solids on evaporation
Bunter	Papplewick Waterworks*	0.018 gm. per 100 c.c.
Magnesian Limestone	Annesley well*	0.0668
Keuper Marl	Well at Newark†	0.188 "

* Data kindly supplied by the Chief Engineers to the Nottingham Corporation and the Basford Rural District Council.

† *Victoria County History of Nottinghamshire*, p. 29.

(2) *The burrowing of rabbits*, which bring large quantities of subsoil to the surface of heaths, arable land, hedgerows and woods.

(3) *Wind erosion*. The lightness of the soil makes it a "blowing sand." Wind erosion is especially noticeable during a dry spring, when the east winds, usually prevalent in March, carry clouds of dust across the fields. A great deal is stopped by the hedgerows, and at this time the hedgebanks frequently have the appearance of sand dunes. Insufficient use is made of shelter belts by means of which the effects of erosion and evaporation by the wind could be reduced. Long narrow strips of pine plantation are numerous in places, and the larger plantations also give protection to adjoining fields. It may be suggested that the extensive felling of the war period, if not soon followed by replanting, will appreciably lessen the fertility of the soil in certain areas, low as it is already.

(4) *Surface denudation by heavy rainstorms*. This is a feature well known

on the Bunter, though "up to the present very few facts bearing upon this subject have been collected" (18). Normally, there is very little surface drainage, about one-third of the rain being absorbed and from 0.5 to 0.6 lost by evaporation. But during heavy rains, the surface becomes saturated very quickly, and torrents of short duration carry the soil down the slopes to the valleys below. About twenty years ago, during a thunderstorm, the rain carried so much earth down the Robin Hood Hills to the mining village of Annesley, that working parties with carts and shovels were employed in clearing it out of the dwelling houses. On August 7th, 1922, 3.86 in. (98 mm.) of rain fell in the Nottingham district in 24 hours. Ploughed fields on the slopes of the hills suffered tremendously, the crops, such as turnips, being removed *en masse*. At Caudwell Dam, near Sutton-in-Ashfield, a channel a foot (say 30 cm.) wide and about a yard (*c.* 1 m.) deep was formed down the hillside, and the detritus from the field and channel was carried into the lake, giving rise to a delta of soil 10 yds. (say 9 m.) across and extending 10 ft. (say 3 m.) out from the margin.

The following table summarises the results of the analysis of seven cultivated soils and their subsoils, typical of the Bunter, and are given to illustrate their general character. In Goodwin's opinion "these soils would appear to be very near the limits within which ordinary cultivation can profitably be carried out" (9).

Table III. *Analyses of Bunter soils* (9).

	Surface soils		Subsoils	
	Average	Range	Average	Range
Mechanical analysis				
Fine gravel	1.65	0.47- 3.64	0.96	0.3 - 2.0
Coarse sand	64.31	53.79-74.98	66.89	53.94-77.47
Fine sand	22.58	11.23-31.32	21.57	10.62-33.16
Silt	2.51	1.98- 4.34	2.58	1.55- 4.66
Fine silt	3.65	0.82- 5.47	2.74	0.66- 5.19
Clay	0.27	0.15- 0.41	0.47	0.31- 0.64
Moisture	1.07	0.70- 1.82	0.86	0.64- 1.02
Loss on solution	1.73	1.22- 2.33	1.77	1.08- 2.75
Loss on ignition	3.26	2.35- 5.28	2.34	1.34- 3.38

	Surface soils		Subsoils	
	Average	Range	Average	Range
Chemical analysis				
Total potash (K_2O)	0.0445	0.012-0.048	0.0162	0.007-0.0476
"Available potash" (K_2O)	0.00236	0.001-0.004	—	—
Total phos. acid (P_2O_5)	0.1165	0.078-0.147	0.0753	0.058-0.100
"Available" phos. acid (P_2O_5)	0.0257	0.003-0.054	—	—
Nitrogen	0.117	0.101-0.140	0.079	0.07 -0.091
Lime as carbonate	0.1468	0.025-0.37	0.220	0.050-0.73

Finally, it is interesting to compare the soils of the Bunter with those of the Bagshot Sands (Eocene) in the South of England, which bear a similar heathy flora. The latter are finer grained than the Bunter and contain more clay, whilst the lime content is slightly higher. The Bagshot area has approximately the same rainfall as that of the Bunter.

Table IV. *Composition of the soil of the Bagshot Beds.*
(*Encyclop. Brit.* 11th Ed., Article "Soil.")

Coarse sand	32 %	Nitrogen	0.19 %
Fine sand	40	Phosphoric acid	0.18
Silt	12	Potash	0.19
Fine silt	8	Calcium carbonate	0.23
Clay	8					

THE FLORA OF NOTTINGHAMSHIRE¹

The most recent account of the local flora is that given by Prof. J. W. Carr in the *Victoria County History*. Of the 1660 indigenous species of Phanerogams and Vascular Cryptogams, as given in the 9th edition of the *London Catalogue*, only 854 are found in Notts., a number less than those of the adjacent counties. The absence of uplands of any considerable height and the fact that the county has no coast line will account for the absence of about 350 species. The Nottinghamshire flora has therefore only 65 per cent. of the species which are known to occur in the inland lowland flora of Great Britain. This is due to various causes, such as:

A. Lack of variety in the physical conditions.

B. The high state of cultivation of most of the area. The only extensive uncultivated districts are on the Bunter, the soil of which, being dry and having an acid reaction, possesses but a scanty flora. There has also been a considerable conversion of arable land into pasture.

C. The absence of marsh and bogland, and of large natural sheets of water. Lacustrine plants are usually absent from the well-kept park lakes.

D. The growth of industrial towns, the sinking of deep wells and collieries which has led to the lowering of the water table, and the drainage and disappearance of what little bog there was.

E. The Magnesian Limestone has not so rich a flora as the other important limestones of Great Britain.

F. To these factors there must be added the pollution of the atmosphere by smoke and the toxic effects of sulphur dioxide and hydrogen sulphide, particularly on the Cryptogamic flora (12). These injurious influences are becoming intensified by the eastward extension of the coalmining area, and the industrialisation of the rural districts. When it is borne in mind that the future development of the mining industry in the centre and north of the county is expected to provide for a new population of about 200,000, the fate of much of the existing natural vegetation is not difficult to foresee.

SHERWOOD FOREST

The sterility of the Bunter soil is chiefly responsible for the fact that considerable portions still retain a primitive form of vegetation, the remnants

¹ Mainly summarised from Carr (5).

of the ancient Royal Forest of Sherwood. The forest was about 25 miles (40 km.) long and from 8 to 10 miles (13 to 16 km.) wide, with an area of about 100,000 acres. It was a royal forest before the Conquest, but the first recorded "perambulation" was that of 1232, and shows that except in two localities, Sherwood was confined to the Bunter outcrop. In the district west of Mansfield, the forest extended on to the Magnesian Limestone, and in the south-east, between Nottingham and the Dover Beck, on to the Keuper Waterstones and Marl. According to Evershed¹, it was "not all of one monotonous character, like some of the deer forests of Scotland, but diversified and picturesque, partly in timber, partly in extensive tracts of heather, gorse or broom."

The survey of 1609 gives the following details:

Inclosures	44,839 acres	Bestwood Park	3672 acres
Woods	9,486 "	Clipstone Park	1583 "
Enclosures	35,080 "	Bulwell Park	326 "
	<hr/> 89,405 "	Nottingham Park	129 "

Clipstone Park was destroyed during the Civil War; "not a tree was left standing." After the Restoration, more than 4000 acres in the north were transformed into ducal parks, but Birklands and Bilhaugh remained in the possession of the Crown until 1800. The Enclosure Acts, 1789-1796, brought 8248 acres into cultivation, chiefly on the western border. Finally, Sherwood passed to the Lords of the Manor and ceased to be a Royal Forest; the greater part of it is now taken up by the estates of Welbeck, Clumber, Rufford, and Thoresby, in the "Dukeries," and Annesley, Newstead, Papplewick, Sherwood, and Bestwood, further south.

VEGETATION OF THE BUNTER SANDSTONE

(1) THE DRY OAKWOOD CONSOCIATION.

The primeval oakwoods of Sherwood are best seen at Birklands and Bilhaugh, north of Edwinstowe. Their ancient condition was described by Camden, the historian (2), as "one close continued shade with the boughs of the trees so entangled in one another that one could hardly walk single in the paths. . . . The forest is sadly altered now, only a few vestiges of its olden glories still survive. . . . At Bilhaugh, are oaks that cannot be less than six or seven centuries old." Cox (7) says that in 1680, "although there were many thousand standing trees, few there were but what were decaying, and very few useful for the navy." In 1794, according to Lowe, there was here "an *open* wood of large oak, but mostly decayed or stag-headed" (11).

In an area of 1487 acres, there were

in 1609, 49,909 oaks (including hollow trees);

in 1686, 37,316 oaks;

in 1790, 10,117 oaks.

¹ *Journal of Forestry*, 3.

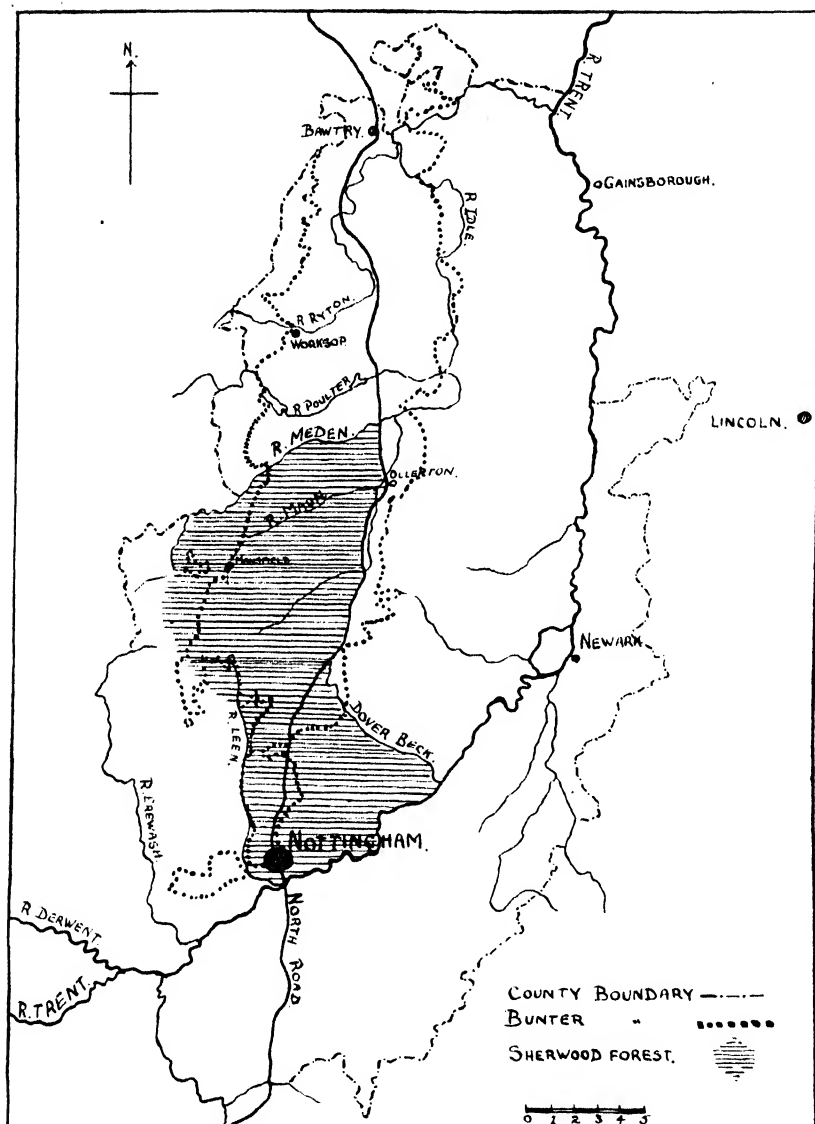


Fig. 2. Sketch map of the County of Nottingham, showing the extent of the Royal Forest of Sherwood in the 13th century, and its relation to the outcrop of the Bunter Sandstone, the River Trent, and the Great North Road (based on a map by Swinnerton, 17).

Thus in a period of one hundred and eighty years, of these fifty thousand trees, four-fifths were cut down. In consequence of this intensive felling, the woodland varies very much in character, showing all stages between open "park"—here grass heath dotted with trees—open oak-birchwood with a grass-heath ground flora (Pl. I, Phot. 1), and closed oakwood or birchwood with a monotonous undergrowth of bracken.

In places, young oaks have recently been planted (wired against rabbit attack) to fill up the canopy, and since it is likely that this policy has been followed for many years, there seems no doubt that large numbers of the trees in these woodlands have been planted. Furthermore, a natural aspect due to their irregularity of position is no criterion of spontaneity. Various existing plantations of oak and chestnut were laid out in 1825, 1833 (the Greendale Oaks) and 1848, to mention a few definite dates, but there are records of extensive planting as early as 1726. Areas left bare by the cutting of timber during the late war reveal the presence of isolated scattered "stag headed" and hollow "giants." Hence, from this practice of sparing the venerables, it follows that these old trees are, in some parts, the only survivors of the natural oakwoods, and all the woods comprising young trees and those of moderate age, i.e. 200 years! or less, are "seminatural."

The ancient oaks are still very numerous. Some, like the Major Oak, are short trees with boles of tremendous girth and extensive crowns: one at Shireoaks is said to have given shelter to 230 horsemen! The other type, which is more abundant, grew in close canopy, for their boles have great height as well as girth.

The woodland varies considerably in regard to the dominant species. A complete census of the old oaks would be interesting as giving some indication of the composition of the original forest, but it was not possible, even after much labour, to identify more than a relatively small number of trees, and it is not suggested that a precise value should be attached to the figures given here. Of 242 ancient oaks examined, 35 per cent. were found to be *Quercus sessiliflora*, 57.4 per cent. *Q. robur*, and the remainder (7.6 per cent.) hybrids. Of 318 younger trees examined at Birklands, 53.8 per cent. were *Q. sessiliflora*, and 40 per cent. *Q. robur*. Most of the durmast oaks belong to the variety (*b*) *pubescens* (Loudon), though the variety (*a*) *genuina* (Willkomm) also occurs. The hybrid *Q. robur* × *sessiliflora* has not hitherto been mentioned in any published record as occurring in the county, and Nottinghamshire does not appear in the list given by Moss in *Journ. Bot.* 1910, p. 34.

The following table shows some of the more striking variations in the distribution of the oaks, and whilst either *Quercus robur* or *Q. sessiliflora* may be locally dominant, with the other absent, sub- or co-dominant, there is some indication that the durmast oaks are now more numerous than formerly.



FIG. 3. Ground vegetation and litter of young Birchwood, Annesley Forest, *Ithyphallus impudicus*, *Pteridium aquilinum*, *Rumex acetosella*.



FIG. 1. Primitive Oak-Birchwood at Birklands, near Edwinstowe. Open canopy: *Quercus robur*, *Q. sessiliflora*, *Betula pubescens*, *Pteridium aquilinum*, *Deschampsia flexuosa*.



Table V. *Variations in the dominant species in the dry oakwoods.*

Locality	Relative age	<i>Q. robur</i>	<i>Q. sessiliflora</i>	Hybrids
Birklands, south side ...	Young	45	3	2
	Old	96	58	12
Birklands	Young	30	26	0
Birklands, N.W. of Major Oak	Young	2	54	9
	Old	—	5	—
1848 Plantation	Young	6	35	3
	Old	3	1	—
Thieves' Wood Plantation	Young	30	74	7
Strawberry Hill Plantation	Young	19	48	1

NOTE. The terms "young" and "old" are used in the above list merely to differentiate between the ancient trees and those of more recent date.

BIRCHWOOD.

The birch, *Betula pubescens* (= *B. tomentosa*) is always present to a greater or less extent in Birklands (i.e. Birchlands) and Bilhaugh, and much of the primitive woodland may be described as oak-birchwood in which *Q. robur* and/or *Q. sessiliflora* are dominant or co-dominant, and *B. pubescens* frequent to sub-dominant.

Although nearly absent from some of the *sessiliflora* woods, yet self-sown birches abound in lines along the rides. Seedlings compete with *Calluna* and with grass-heath species, whilst older plants about 4 ft. high are common. Birches also occur frequently along the margins of the pine plantations. One factor affecting the propagation of *B. pubescens* from seed is the light intensity, for removal of the oaks results in the formation of a more open canopy, and the increase in abundance of the birch. Ultimately pure birchwood may develop, and frequently forms a much closer canopy than the oak-birchwood.

Pure birchwood also occurs on Drift gravels just to the north of Ollerton. The boundaries of these patches of drift are indefinitely marked on the 1 in. Geological Map, and possibly they may be more extensive. The one to the west of the Worksop road is occupied by grass heath, but the other is covered with pure birchwood in close canopy (Pl. I, Phot. 2). A gravel pit shows the presence of a stratum of quartzite pebbles at the top of the subsoil, about 12 to 18 in. (say 30 to 45 cm.) below the surface. The boulders are sufficiently close to make this conglomeratic layer an obstacle to the growth of roots and to the capillary uplift of water from below. Hence the absence from these gravels of deep rooting trees like the oak, and the abundance of the birch, a shallow-rooting species capable of thriving on the dry soils.

Apart from the region between the Maun and the Meden, it is doubtful whether any primitive woodland remains, though individual trees of great age still persist in some localities, e.g. the Pilgrim Oak at Newstead and Haywood Oak near Blidworth. In 1624 there was a destructive forest fire, which was finally put out by the changing of the wind, "as the fire was approaching the northern end of the great long wood that then stretched from Mansfield to Nottingham" (5). This district is still well wooded, despite the

extensive felling of 1914 to 1918, and Noman's Hill Wood, Thieves' Wood, Harlow Wood, Kighill Wood and others were investigated.

Noman's Hill Wood, forming part of the Portland Estate, is apparently the area of which Major Rooke wrote in 1799, "The Marquis of Titchfield had sown upwards of a hundred acres in parts of the old forest between Mansfield and Nottingham with acorns¹." In the portions now remaining, the oaks are from 6 to 30 ft. apart in rows about 20 to 45 ft. apart. They are in close canopy along the rows, but open sky frequently appears between them. The trees are tall with thick straight boles, rather large for use as pit-prop timber, for which purpose parts of this and other woods in the district were cut during the war, the trees used often being small and stunted. *Q. robur* is the dominant species, but *Q. sessiliflora* is fairly abundant, and the hybrid occasional². *Betula pubescens* occurs frequently, in all stages from seedlings to trees as high as the oaks. The former are common on and alongside the rides. The older birches are more abundant along the margins of the wood than in the interior; they are situated irregularly with reference to the tree rows and have obviously originated spontaneously.

Small areas of pure birchwood are to be found, and their number is increasing owing to the extensive felling of the war period.

This plantation-like appearance is less marked in the case of Harlow and other oakwoods, for they are more open, and the birch is sub-dominant; they approximate in form to the oak-birchwood of Birklands.

The Spanish chestnut, *Castanea sativa*, is found in most of the mixed plantations and semi-natural oakwoods of the Bunter, and there is a fine avenue of these trees in Thoresby Park. Although the chestnut is certainly not indigenous to these soils, yet there is ample evidence that it can spread naturally from seed. Beech societies occur in several localities: one in Hagg Wood on the Newstead Estate (? planted by the poet Byron), where the trees are well grown and cast a shade dense enough to inhibit the growth of ground vegetation. The famous beech avenue near Ollerton should also be noted. It is doubtful whether the beech society actually exists on the Bunter as a naturally occurring plant community (cf. *Types of Brit. Veg.* p. 93), for the species has been planted extensively since 1726.

The Shrub Layer.

The most striking fact about the undergrowth of the dry oakwoods is the entire absence of coppice, and the scantiness of the shrub layer in general. *Lonicera periclymenum* is abundant, and in this habitat, adopts a decumbent habit, owing to the absence of erect shrubs that might furnish supports suitable for climbing. In these situations the honeysuckle never flowers, nor in the open after the felling of the trees, but in the hedgerows it grows normally

¹ *Sketch of Sherwood Forest*, 1799.

² Note that in Thieves' Wood (Table V) *Q. sessiliflora* is dominant.

and flowers abundantly. *Crataegus*, *Ilex*, *Sambucus* and small oaks, chestnuts, and birches are occasionally met with. *Rubus fruticosus* and *R. Idaeus* are frequent, but are generally less robust (especially the latter) than in marginal or open situations. These, with *Ulex europaeus*, *Cytisus scoparius*, and *Prunus spinosa*, belong rather to the scrub than to the oakwood.

The Ground Vegetation.

The ground vegetation shows the same paucity of species as the shrub layer and is characterised by the overwhelming luxuriance of bracken (*Pteridium aquilinum*) which occasionally reaches a height of 5 ft. Where the dry oakwood has a close canopy, the bracken is practically continuous, and is an important factor in the vertical stratification of the woods, which usually have a light open appearance, owing to the absence of coppice and to the position of the *Pteridium* below the eye level, so that one can see a comparatively long distance. But so much light is absorbed by the bracken that the floor of the wood is generally bare. Actinometer observations show that in oakwood and in birchwood in close canopy, 7.3 to 53 per cent. of the diffuse light reaches the bracken layer, whilst only 0.4 to 10 per cent. reaches the soil, the mean value being less than 5 per cent. In other words, from 73 to 98 per cent. of the light falling upon the bracken "stratum" is absorbed by it, the higher numbers predominating where both canopy and bracken are close and continuous.

Observations on closed *Pteridium* societies on the heaths confirm this result, the bracken alone, in the absence of trees, being able to absorb as much as 98 per cent. of the light. The shrub layer is very poor in individuals as well as in species, and, as a light-absorbing foliar canopy, is non-existent in these woods, in which the *Pteridetum* virtually fills the rôle of the coppice of the damp oakwood and ash-oakwood. It does not cast quite so deep a shade, however, as the coppice.

The effect of the alternation between the "light phase," from autumn to spring, and the "shade phase," from leaf expansion to leaf fall, is less marked in these woods than in damp oakwood. *Pteridium* gives rise to a xerophytic type of humus, or rather of dry debris that covers the ground all through the winter to a depth of several inches. Other factors contributing to this slow rate of decay are the relatively small rainfall and the low water and lime contents of the soil. Even oak and birch leaves persist from autumn to autumn in masses where they fall, held by the petioles of the bracken. The importance of the "debris factor" will be discussed in detail later.

With no coppice to be removed periodically, there is never any drastic change in the lighting of the woods, and the ground surface is almost continually subject to light of small intensity for many years. Hence, in the absence of any periodic stimulus to the ground flora, it is not surprising to find that *Pteridium* in "close canopy" is unaccompanied by any other species

whatever, not even *Holcus mollis* or *Scilla*, though the former is abundant wherever the bracken layer becomes scattered, and the latter is rare to occasional, never locally sub-dominant in any *typical* dry oakwood, thus far examined on the Bunter.

In a birchwood at Birklands, a considerable amount of bracken had been cut, enabling a careful examination of the surface to be made. The soil was covered with leaf debris over about 2 in. of humus, and was practically devoid of what may be called "minor ground vegetation"; but a *few* isolated attenuated plants were present, including *Galium saxatile*, *Deschampsia flexuosa*, *Holcus mollis* (none of them flowering), and *Potentilla erecta* and *Rumex acetosella* in flower.

Occasional fires in dry years and the cutting of the bracken lead to the removal of the leaf debris and an increase of light during the shade phase, and so give the "periodic impetus" to small areas of woodland. The result is the temporary establishment of a ground flora similar to that of the margins of the woods and the sides of the rides, and consisting chiefly of the above-named species. It must be noted, however, that the fires also destroy the humus and the plants whose root systems are almost confined to it (*Galium saxatile*, *Holcus mollis*, etc.), and that the bracken is the least affected, since its rhizomes are situated more deeply in the soil. The species that such fires do let in are ruderals like *Rumex acetosella*, *Poa annua*, and *Capsella*, and seedlings of *Ulex europaeus*, *Cytisus scoparius*, *Sambucus* and *Digitalis*.

Humus and soil. The humus layer ranges in depth from $1\frac{1}{2}$ to $3\frac{1}{2}$ in., and, as has been said, is generally covered with leaf debris, more or less dry. It is not well decayed, for its plant structure is recognisable a year or more after leaf fall, and on the whole it is rather chaffy. The abundance of Basidiomycetes (Pl. I, Phot. 3) testifies to its sourness and it always gives an acid reaction. The natural water content has not yet been determined, but it is obvious that differences do exist, influenced in part by the depth of the water table. The presence in a Birklands birch grove, of a pool with *Ranunculus flammula* and *Heleocharis multicaulis* (pH 5.5 approx.) and the occurrence of *Leucobryum glaucum* (pH 4) in *Quercetum sessiliflorae*, with *Nardus* bordering the rides, shows the comparatively higher water content of the soil of that district.

The Marginal and Ride Flora.

These parts of the woods are usually well lighted, and are characterised by the presence of *Deschampsia flexuosa* and other grass-heath species which can endure a fair degree of shade. 80-85 per cent. of the plants occurring here are members of the grass-heath flora. *Pteris* is usually absent from the rides and is very open in the marginal habitats. *Calluna* and *Nardus* are frequently found alongside the rides: *Juncus* spp. and *Ranunculus repens* on the paths, where *Luzula campestris* also thrives well. Birch seedlings are abundant and become well established along the margins.

In these situations the herbaceous plants flower well, especially those which are frequently found in a non-flowering state among the *Pteridetum*. In the more open oak-birchwoods, this marginal flora is extensively developed, forming a *Pteridium-D. flexuosa* society which may occupy the entire floor of the wood.

The Relation between the Woodland Trees and the Ground Flora.

The "oak-birch-heath" that fringes the dry oakwood of Birklands is dotted with oaks and birches, singly or in clusters. Where the trees are fairly near together, *Pteridium* is dominant, being practically continuous, with *Deschampsia flexuosa* sub-dominant beneath it; but where they are from 50 to 80 yds. distant, *D. flexuosa* dominates the "heath," and the bracken is reduced to a zone bordering the trees. This area has certainly been occupied by dry oakwood, and the disappearance of the once continuous covering of bracken was accompanied by the establishment of a closed, and in parts relatively pure, *D. flexuosa* society (Pl. I, Phot. 4). The factors involving the decline of the oakwood ground flora in the face of the progressive grass-heath species may here be studied under particularly favourable conditions, for since the felling of the woods, this part of Sherwood has suffered little by the interference of man. The oaks are aged trees of the "open" type, with boles of great diameter and extensive crowns that reach down to the ground. *D. flexuosa* stops short on the outer edge of the foliar zone (light intensity = 20 per cent.) in which *Pteridium* is dominant, accompanied by *Holcus mollis* and *H. lanatus*, thinly scattered amongst the dry leaf debris, this being held in position by the bracken and the oak branches. Around the bole is a wide zone, clear of debris, usually occupied by *D. flexuosa*, here generally not flowering (light intensity = 12½ per cent.). This distribution of the ground flora was found to be the same under numerous oaks (*Q. robur*) and under *Acer pseudoplatanus*, occasionally planted. *D. flexuosa*, however, is absent from beneath groups of *Pinus sylvestris* where a quarter-inch layer (6 mm.) of dry pine needles covers 2½ in. (6 cm.) of humus, but the vegetation fringing the trees is exactly the same.

The birches are surrounded by closed bracken societies, but the diminution of the light does not prevent *D. flexuosa* from developing continuously beneath, right up to the trunk. The debris does not accumulate here to the same extent as under the oak, and *Holcus mollis* is less abundant or absent.

Under the tall oaks of the oak-birchwood, a ring of bracken closely invests the bole, covering much dry humus and leaf debris. *D. flexuosa* dies out at the edge of this *Pteridium* society, beneath which nothing grows.

The light intensities of *Deschampsia flexuosa* habitats were found to range from 2.4 per cent. to 100 per cent., but in most situations where the illumination falls below 12.5 per cent. (occasionally even at 25 per cent.) the grass does not flower, though even here it may form a continuous turf. In the oak

and birch woods, along the inner boundary of the *D. flexuosa* marginal societies, the illumination of those situations from which the grass is absent—i.e. where the dry leaf debris accumulates in the open scattered Pteridetum, and where the carpet of heath-grass breaks up into “islands” among the undecayed humus—varies from 14 to 62·5 per cent. It is clear that light intensity is not the factor which directly determines the distribution of the heath grass in these habitats.

Where the dry oakwood is in close canopy, *Pteridium* forms a closed society right up to the edge of the rides, but differences have been observed according to the height of the trees. If the canopy is low, the Pteridetum extends to its edge, and grass-heath plants and *Calluna* do not cross the debris line: when the canopy is high, *Pteridium* does not extend beyond the line of the boles and *D. flexuosa* meets it there.

Hence it is concluded that the master factor limiting the distribution of the ground flora in the dry oakwood is the slow rate of decay, leading to the accumulation of dry humus (up to a thickness of 4 in.), and loose leaf debris (9 in.), which is fatal to the existence of carpet plants and geophytes, and to the germination of seeds. As has already been pointed out, it reduces the illumination during the “light period,” and the result of its prolonged action is the entire disappearance or absence of plants which are not specially adapted to these conditions. It also explains the overwhelming dominance of *Pteridium* which, by reason of its deep rhizome, circinate vernation, and the length and strength of its petiole, is perfectly fitted for life in such a habitat.

On the other hand, when the wood becomes open there is less dry debris, and *D. flexuosa*, *Galium saxatile*, and other grass-heath species are able to enter, the former becoming sub-dominant. The thick, close, and often tussocky turf that it forms is an obstacle to the free development of *Pteridium*, which becomes scattered, leading to the further reduction of the amount of dry humus accumulated. The invasion of dry oakwood by grass-heath or heathy ground flora is, however, a very slow process, and, as will be seen, even after the disappearance of all the trees, the bracken society can hold its own for a long period.

Holcus mollis. This species is the only other plant which is well adapted to life amid the dry humus. Its shoots can penetrate the humus horizontally and vertically, the stolons being found generally in the top inch. The plant is absent from the closed Pteridetum, but can generally establish itself where the bracken is short and scattered. Although it is a frequent member of the grass-heath community, yet there it gives place also to *D. flexuosa*; which forms a closer turf. *Holcus mollis* must be regarded as one of the few plants really abundant in the ground flora of the Bunter oakwoods.

Habitat Factors of the Oaks.

In Britain, *Quercus sessiliflora* is dominant in woods occurring on shallow siliceous soils (often Palaeozoic) and on limestone soils from which the greater

part of the lime has been leached out. The Bunter is typical of those deep (often Mesozoic) sands where *Quercus robur* and *Q. sessiliflora* are co-dominant, and on which either may be dominant.

The edaphic conditions of *Quercetum sessiliflorae* in general are also prevalent here (i.e. a low lime content, a low soluble mineral content and the accumulation of acidic humus); but owing to the softness and friability of the underlying rock the soil is deep, and this constitutes an essential difference between the Bunter and the older siliceous sandstones. Depth of soil is regarded by Moss as a factor of great importance in determining the dominance of *Quercus robur* or *Q. sessiliflora*. Salisbury (15) concludes "that the contrast with woods of *Q. robur* depends, at least partly, on a higher acidity corresponding with a lower content of soluble mineral salts and of water." At Birklands, there are signs that the water is nearer the surface than is usual on the Bunter, and the consequent higher water content and diminished aeration may also lead to a higher degree of acidity in the soil. Again, leaching tends to remove the basic constituents of the soil, and where it is excessive, may be accompanied by a corresponding change in the vegetation from a more basic to a more acidic type. The suggestion is made that *Quercus robur* has grown less abundant, and *Q. sessiliflora* more abundant on these deep sands as the acidity of the soil has increased, a change that may be regarded as the initial phase in the degeneration of the woodland and the development of heath. It is hoped that further investigations of the habitats of the two species as to the water content, acidity, and shallowing of the soil owing to the formation of pan, will shed more light on the problem of their distribution, which in the absence of more definite evidence cannot be adequately discussed.

The Plantations.

The extensive tree felling of the eighteenth century was the cause of the disappearance of many of the oakwoods of Sherwood, but it is interesting to note that the Report of the Board of Agriculture of 1794 on Nottinghamshire declares that "a spirit of planting had prevailed throughout Sherwood for forty years," and gives details regarding afforestation at Welbeck, Clumber and Rufford. At Welbeck, in 1726, there was extensive planting of oak, beech and chestnut with fir and larch to act as nurseries: later, pure oak plantations were laid out for timber and bark. "Oak does best in mixed plantations with just enough beech to shade it¹." In Newstead Park the Lord Byron of the day cut down oaks wholesale to the value of £60,000, and a large part of the estate was turned into farms. Recent owners of the property have found these unprofitable (i.e. since the repeal of the Corn Laws) and considerable areas have been planted with conifers. During the past half-century there has been a marked increase in the area devoted to woodland in Nottinghamshire, this reaching 30,433 acres in 1905¹.

In addition to the semi-natural oakwoods already described, the plantations now in existence are of two main types, mixed woods composed largely of deciduous species with a few conifers, and pine and larch plantations.

THE DECIDUOUS PLANTATIONS.

Only a few woods of this type on normal Bunter soil were investigated, and even these, situated chiefly south of Mansfield were very small, the largest plantations having been felled during the

¹ *Victoria County History of Nottinghamshire* (Forestry).

war. On many hilltops, and on the Bunter escarpment where the steep slope of the ground makes cultivation difficult, small plantations exist, but these in several cases are degenerating into scrub, the trees being past their prime. On the other hand, Coxmoor Wood near Kirkby and Little Oak Plantation at Annesley, attracted attention on account of their soils, which are more loamy than usual, and in which the humus is well decayed.

The pedunculate oak (*Q. robur*) is the most abundant tree, but the chestnut, beech and sycamore are also very common, together with *Pinus sylvestris* and other Coniferae. *Q. sessiliflora* is occasionally found in these plantations. The trees are in close canopy and cast a heavy shade: this explains the general absence of birch from the interior of these woods. There is usually no coppice, though *Sambucus nigra* is locally abundant; *Rubus* spp. are abundant in marginal habitats, frequently accompanied by *Lonicera periclymenum*. The shrub layer is hardly more conspicuous here than in the dry oakwoods, though the ground vegetation is more varied. The deeper shade cast by the large leaved trees in close canopy prevents *Pteridium* from becoming abundant, except along the borders of the woods. For this reason the accumulation of dry leaf debris is less marked, but is still the cause, in part, of the scantiness of the ground vegetation in the interior of the woods. The light intensity, even in the shade phase, was rarely found to fall below 5 per cent. (range 3.1 per cent. to 12 per cent., average 6.6 per cent.) a higher figure than that recorded by Salisbury in the case of coppiced woods with a rich ground flora.

The ground flora is best developed in marginal situations alongside the Pteridetum, and in places where there is a break in the canopy. *Scilla non-scripta* is abundant to locally sub-dominant accompanied by *Holcus mollis*, *Galium saxatile*, *Digitalis*, *Oxalis*, *Dryopteris spinulosa*, and *Viola riviniana*; on the loams of the Coxmoor and Annesley woods, these species, with *Circaea lutetiana*, *Ranunculus repens*, *Nepeta glechoma*, *Lychnis dioica*, *Veronica chamaedrys*, *Sanicula europaea*, *Urtica dioica*, *Galium cruciata*, and *Geum urbanum* form numerous small societies, whilst *Arctium lappa*, *Rumex* spp., and *Deschampsia caespitosa* occur frequently. It is apparent that these woods, situated at the base of the Bunter outcrop, show similarities to damp oakwood and are worthy of detailed investigation.

THE CONIFER PLANTATIONS.

The conifer plantations are very numerous throughout Sherwood. The older ones are generally pure pinewoods (*P. sylvestris*), but mixtures with *Picea* and *Larix* are not uncommon. At Bilhaugh large areas have recently been planted with larch, bordered all round by the common pine. Larch canker is prevalent in some districts, and affects even trees a few years old. The pinewoods of Longdale have an abundant mixture of birch, the trees being from 30 to 40 ft. high in close canopy, but in general, *Betula* is only found at the edges of the plantations, where it arises spontaneously and maintains itself well.

These pinewoods present no unusual features: except near the margins, they do not possess a ground flora, though scattered *Pteridium* societies, with *Holcus mollis*, *Agrostis vulgaris* and *Deschampsia flexuosa* are found in the less shady spots, especially where the birches or other occasional deciduous trees let in the light. *Pteridium* also occurs abundantly on the rides, with dead *Calluna*, which had colonised the paths while the plantations were young or before afforestation, but had failed to maintain itself when the growing pinewood reduced the light intensity below its minimum requirements.

Neither seedlings nor young plants of *Pinus* have been found growing naturally, and it appears that in this district, the pine does not propagate itself from seed. Moss regards its lack of prosperity in the Pennines as due to the high rainfall, but the rainfall of the Bunter is not greater than that of the southern heaths which are being successfully invaded by sub-spontaneous pinewood (19).

Regeneration of the Woodlands.

Oakwoods. The factors tending to prevent the natural regeneration of oakwood have been discussed by Moss (13), Watt (20) and others, and to this discussion there is very little to add, except by way of confirmation. Oak seedlings are not found growing under the close Pteridetum, but are frequent

alongside the rides and margins of all the oakwoods and of the mixed plantations where *Pteridium* is weakly developed or absent, and *Holcus mollis*, etc., often abundant.

Young self-sown oaks are occasionally seen in the same situations. It is quite clear that on the Bunter Sandstone, as well as in other parts of England, the birch has a great advantage over the oak in the replacement of retrogressive dry oakwood, or of any associated plant community.

Rejuvenation by means of stool shoots seems to be more successful; and in the case of some woods recently felled, will lead to the formation of oak coppice in a few years' time. In other areas, sycamore and chestnut are rapidly growing up from the stools, but these species are occasionally propagated from seed.

Birchwood. Birchwood is extending or arising spontaneously on the sites of several mixed woods and pinewoods felled in 1915-17. The young birchwood at the Sheepwalk Plantation, on the Newstead estate, was found to have developed chiefly from the stools, and is now dominant over the pre-existing *Deschampsia flexuosa* society, which has almost ceased to flower owing to the increasing shade. On Annesley Forest, the birchwood, now about 10 ft. (3 m.) in height, is self-sown for the most part, though stool shoots are abundant. It is close enough in parts to have killed off all the ground vegetation except *Funaria*. In both areas, seedlings are very abundant, but are frequently of a bushy type, the result of pruning by rabbits. On the Annesley drift gravels, the lateral roots of the seedlings are excessively developed, and run along under the carpet of heath mosses in the top 1-2 in. (2.5-5 cm.) of soil. The spontaneous birchwoods here described show neither the manner nor the rate at which well-established grass heath or Callunetum are invaded by *Betula* from without, as the habitat is being simultaneously competed for by ruderals, by *Calluna*, and by grass-heath plants.

Floristic Composition of the Bunter Woodlands.

TREES:

<i>Quercus robur</i>	f.—l.d.
„ <i>sessiliflora</i>	f.—l.d.
„ <i>robur</i> × <i>sessiliflora</i>	o.
<i>Betula pubescens</i>	f.—l.d.
<i>Fagus sylvatica</i>	o.—l.d. (plantations)
<i>Alnus glutinosa</i>	l.a. (river valleys)
<i>Fraxinus excelsior</i>	r. (at base of Bunter, adjoining Permian Marl)
<i>Sorbus aucuparia</i>	r.—l.a.
<i>Pyrus malus</i>	r.
<i>Acer pseudo-platanus</i>	f. (planted)
<i>Carpinus betulus</i>	r. „
<i>Castanea sativa</i>	o.—f. „
<i>Larix europaea</i>	f.—l.d. (plantations)
<i>Pinus sylvestris</i>	f.—l.d. „
<i>Populus alba</i>	r. (planted)
<i>Tilia europaea</i>	o. „
<i>Ulmus campestris</i>	r. „
„ <i>montana</i>	r. „

Floristic Composition of the Bunter Woodlands (contd.).

SHRUBS:

<i>Betula pubescens</i>	f.
<i>Calluna vulgaris</i>	l.f. (margins and rides)
<i>Castanea sativa</i>	r.
<i>Crataegus oxyacantha</i> (agg.)	f.
<i>Cytisus scoparius</i>	o. (margins)
<i>Hedera helix</i>	r.—o.
<i>Ilex aquifolium</i>	o.
<i>Lonicera periclymenum</i>	r.—f.
<i>Prunus spinosa</i>	r.
<i>Quercus</i> spp.	r.
<i>Rosa canina</i> (agg.)	o. (edges)
<i>Rubus fruticosus</i> (agg.)	r.—f. (l.a.b. in mixed woods)
" <i>idaeus</i>	r.—f. (edges)
<i>Salix caprea</i>	r. (Coxmoor wood, on wet soil)
<i>Sambucus nigra</i>	r.—l.a.
<i>Ulex europæus</i>	f. (margins)
<i>Vaccinium myrtillus</i>	o. (margins, rarely fruiting)
<i>Viburnum opulus</i>	r. (one wood only)
<i>Viscum album</i>	Recently seen on <i>Populus</i> at Budby

GROUND VEGETATION:	Dry oak-birchwood	Mixed woods	Pine woods	Margins	Rides
<i>Achillea millefolium</i>	—	—	—	o.	—
<i>Agrostis vulgaris</i>	o.—f.	f.	—	l.a.	l.a.
<i>Arctium lappa</i>	—	o.	—	—	—
<i>Arrhenatherum avenaceum</i>	—	o. (edges)	—	—	—
(<i>Capsella bursa-pastoris</i>)	r. (after fires)	—	—	—	—
<i>Carduus nutans</i>	—	—	—	—	o.
<i>Cerastium vulgatum</i> (agg.)	—	—	—	—	o.
<i>Circaea lutetiana</i>	—	l.f. (one wood only—wet)	—	—	—
<i>Cirsium</i> spp.	—	—	—	r.	o.
<i>Deschampsia caespitosa</i>	r.	o.	—	—	—
" <i>flexuosa</i>	f.—l.s.-d.	—	—	a.	a.
<i>Digitalis purpurea</i>	o.—f.	o.—f.	—	o.	—
<i>Dryopteris filix-mas</i>	—	r.	—	—	—
" <i>spinulosa</i>	o.l.	f.	o.	—	—
(<i>Erica cinerea</i>)	—	—	—	o.—l.f.	o.
<i>Euphrasia officinalis</i>	—	—	—	o.	—
<i>Galeopsis tetrahit</i>	—	r.—o.	—	—	—
<i>Galium cruciata</i>	—	l.f. (one wood only)	—	—	—
" <i>saxatile</i>	o.—f.	o.—f.	o.	f.—c.	f.
<i>Geum urbanum</i>	—	l.f.	—	—	—
<i>Heracleum sphondylium</i>	—	o. (edges)	—	—	—
<i>Holcus lanatus</i>	—	o.	—	o.	o.
" <i>mollis</i>	f.—a.	f.	f.	f.—a.	f.—a.
<i>Hypericum humifusum</i>	—	—	—	—	o.
<i>Juncus bufonius</i>	—	—	—	r. (wet places)	—
" <i>conglomeratus</i>	—	—	—	o.	—
" <i>effusus</i>	—	—	—	o.	—
" <i>squarrosus</i>	—	—	—	r.	—
<i>Leontodon hispidus</i>	—	—	—	—	r.
<i>Luzula campestris</i>	—	—	—	o.—a.	o.—a.
<i>Lychnis dioica</i>	—	l.f.	—	—	—
<i>Myosotis collina</i>	—	—	—	f.c.	f.c.
(<i>Nardus stricta</i>)	—	—	—	—	f.
<i>Nepeta glechoma</i>	—	l.a.	—	—	—
<i>Oxalis acetosella</i>	—	o.	—	—	—
<i>Plantago major</i> , var. <i>intermedia</i>	—	—	—	—	r.
(<i>Poa annua</i>)	r. (after fires)	—	—	—	o.
<i>Polygonum aviculare</i>	—	—	—	r.	—

Floristic Composition of the Bunter Woodlands (contd.).

GROUND VEGETATION (contd.):	Dry oak- birchwood	Mixed woods	Pine woods	Margins	Rides
<i>Potentilla reptans</i>	—	—	—	f.	f.—a.
„ <i>erecta</i>	o.	o.	—	f.	f.
<i>Prunella vulgaris</i>	—	—	—	o.	o.
<i>Pteridium aquilinum</i>	d.	f.	o.—f. (edges)	f.—s.-d.	o.
<i>Ranunculus repens</i>	—	f.	—	—	o.—f.
<i>Rumex acetosa</i>	—	r.	—	—	—
„ <i>acetosella</i>	o.	o.	—	f.	f.
„ <i>crispus</i>	—	r.	—	—	—
„ <i>obtusifolius</i>	—	r.—o.	—	—	—
„ <i>sanguineus</i>	—	r.	—	—	—
<i>Sagina nodosa</i>	—	—	—	—	o.
<i>Sanicula europaea</i>	—	l.f. (one wood only)	—	—	—
<i>Scilla nutans</i>	r.	f.—l.s.-d.	o. (edges)	—	—
<i>Senecio jacobaea</i>	—	—	—	—	o.—f.
<i>Spergularia rubra</i>	—	—	—	—	r.—o.
<i>Stellaria graminea</i>	—	—	—	o.	—
„ <i>media</i>	—	—	—	—	r.—o.
<i>Teucrium scorodonia</i>	l.f. (in “open” places)	—	—	—	—
<i>Trifolium repens</i>	—	—	—	o.	—
(<i>Trifolium decumbens</i>)	—	—	—	—	r.
<i>Urtica dioica</i>	—	l.a.	—	o.—l.a.	o.—l.a.
<i>Vaccinium myrtillus</i>	r.—o. (non-fl.)	l.f.	—	o.—l.f.	—
<i>Veronica arvensis</i>	—	—	—	—	o.—l.f.
„ <i>chamaedrys</i>	—	l.a.	—	r.	r.
„ <i>officinalis</i>	—	—	—	r.	—
„ <i>serpyllifolia</i>	—	—	—	o.	o.—l.f.
<i>Viola</i> spp. (<i>riviniana</i>)	o.	l.a.	—	o.	—

(2) THE SCRUB ASSOCIATION.

The scrub association is found on the commons and warrens, but is most extensively developed by the waysides, which, in Sherwood Forest, are usually as wide as the roads themselves. Except for occasional fires, this wayside flora has suffered little damage by man, and as a habitat of relatively constant edaphic characters must be considered very old. There has consequently been plenty of time for natural changes in the vegetation to become well established by colonisation and succession, and it is not surprising to find that the scrub association has to compete with grass heath and *Calluna* heath, and with ruderals, which occupy patches of bare soil. Spiny shrubs such as *Rosa* spp., *Rubus* spp., *Crataegus*, and *Prunus spinosa* are abundant, but *Ulex europaeus* is easily the leading dominant. *Pteridium*, *Cytisus scoparius*, and *Lonicera* are also abundant, together with many herbaceous plants which can flourish in the shelter and relatively slight degree of shade of the scrub. On the other hand, where *Ulex* forms pure societies, it frequently becomes extensive and close enough to drive out the ground flora entirely. Its recovery after fires seems to be rather more rapid on the wayside habitats than on the commons, probably owing to the more efficient dispersal of the seeds, and to a greater degree of freedom from the attacks of rabbits. The Ulicetum is a vigorously

progressive society; it has successfully colonised the sandstone "cliffs" and slopes of railway and road cuttings, and there is no indication that *Pteridium* is replacing it on the waysides. In fact, the bracken survives principally on the borders of the scrub and *Ulex* societies and along the hedgerows, and though fires are frequent, giving *Pteridium* an advantage for the following few years, there are not many wayside stations where it remains dominant. The re-colonisation of grass heath and scrub after a recent fire is being watched at several places on the Robin Hood Hills. It has been noticed that the gorse stumps which are overgrown with bracken are recovering more rapidly than others in the open, having longer and better developed shoots, due in part to less intense light, greater humidity, and less exposure to wind and to the depredations of rabbits. Owing to the herbaceous nature of the young shoots, protection by the surrounding vegetation is advantageous.

On Annesley Forest, where *Ulex* is exposed to rabbit attack in the open, the small plants are of the cushion type, and older plants are normal, i.e. erect above, with a cushion-like base; but close by, even young self-sown birches form a sufficient screen, and the gorse has escaped attack altogether.

Hence the scrub association is characterised by the shrubs of the marginal oakwood, which flourish much better after the removal of the trees. The *Pteridetum* and the ground flora of the oakwood remain to compete with the scrub, and there is evidence to show that these plants can retain their position for a very long time, assisted in part, by the fires that hinder the progressive formation of *Ulicetum*, or in situations where the grass heath cannot be easily developed. There is a local "tradition" that the Robin Hood Hills have always been treeless, this being based apparently on Byron's poem, beginning "Hills of Annesley, bleak and barren" (1805), but their character is due to the action of a former Lord Byron, who, in the eighteenth century, cleared the timber from the western part of the Newstead estate. After a century and a half these slopes are still dominated by *Pteridium* (1-2 ft. high), *Holcus mollis*, *Teucrium scorodonia*, and *Lonicera periclymenum* on the one hand, and abundant *Ulex* (last fired in 1921 and as yet not much in evidence), with *Sambucus* and *Crataegus*, representing the scrub flora on the other. The steep slopes are much affected by rainwash, and the rhizomes of the bracken are sometimes so near the surface that they have also been destroyed by fire. Grass heath, however, has established itself on level ground at the base and crest of the hills, and on the adjacent Mosley Hills, which are less steep. In the past, some of this land was farmed or grazed, but now forms part of the Hollinwell golf course. Although *Pteridium* has disappeared from the Mosley Hills, *Holcus mollis* still persists, and marks in one place the line of a hedgerow (the "linear extension of a wood") after all traces of hawthorn, scrub, bracken and hedgebank have entirely disappeared. Here indeed, in the *Holcetum mollis*, we see the last vestige of the woodland flora.

Hence it is clear that in considering the interaction of *Pteridium* and *Ulex*

europaeus, or rather of the scrub association and the woodland ground flora, the effect on the latter of the dominant grass-heath species, *Deschampsia flexuosa*, must also be taken into account.

The Scrub and Wayside Flora.

SHRUBS.

<i>Ulex europaeus</i>	f.—l.d.	<i>Rosa arvensis</i>	o.
<i>Crataegus oxyacantha</i> (agg.)	a.	" <i>canina</i> (agg.)	f.—a.
<i>Cytisus scoparius</i>	o.—f.	<i>Rubus fruticosus</i> (agg.)	a.
<i>Ilex aquifolium</i>	o.	" <i>idaeus</i>	f.—l.a.
<i>Lonicera periclymenum</i>	o.—f.	<i>Sambucus nigra</i>	o.
<i>Prunus spinosa</i>	o.		

ASSOCIATED HERBACEOUS SPECIES.

<i>Pteridium aquilinum</i>	f.—l.d.	<i>Lychnis alba</i>	r.
<i>Agropyrum caninum</i>	l.f.	<i>Nepeta glechoma</i>	l.a.
" <i>repens</i>	l.f.	<i>Pimpinella saxifraga</i>	l.f.
<i>Anthriscus sylvestris</i>	o.	<i>Polygonum convolvulus</i>	o.
<i>Aroctium lappa</i>	r.	<i>Plantago lanceolata</i>	f.
<i>Arenaria serpyllifolia</i>	l.f.	" <i>major</i>	f.
<i>Arrhenatherum avenaceum</i>	a.	<i>Prunella vulgaris</i>	f.
<i>Calamintha clinopodium</i>	r.	<i>Ranunculus repens</i>	f.
<i>Campanula rotundifolia</i>	f.	<i>Rumex acetosella</i>	o.—f.
<i>Centaurea nigra</i> (agg.)	f.	<i>Sagina procumbens</i>	l.f.
" <i>scabiosa</i>	o.—f.	<i>Senecio jacobaea</i>	o.—f.
<i>Chaerophyllum temulum</i>	f.	<i>Silene inflata</i>	r.
<i>Digitalis purpurea</i>	o.	<i>Sonchus asper</i>	o. (ruderal)
<i>Galeopsis tetrahit</i>	o.—f.	<i>Stachys sylvatica</i>	l.a.
<i>Galium aparine</i>	f.	<i>Stellaria graminea</i>	f.
" <i>cruciata</i>	l.f.	<i>Tamus communis</i>	o.—f.
<i>Geranium robertianum</i>	r.—l.f.	<i>Teucrium scorodonia</i>	l.a.
<i>Heracleum sphondylium</i>	f.	<i>Trisetum flavescens</i>	r.
<i>Holcus lanatus</i>	o.	<i>Urtica dioica</i>	f.
" <i>mollis</i>	a.	<i>Vicia cracca</i>	f.
<i>Hypericum perforatum</i>	l.f.		

This list does not include the wayside species which belong to the heath and grass-heath communities, but only those strictly associated with the scrub.

(3) THE GRASS-HEATH ASSOCIATION.

Grass heath is widespread on the Bunter Sandstone and has originated in a variety of ways:

(1) Land which has passed out of cultivation is rapidly overrun by grass-heath plants: arable land in the third year of rotation (i.e. second year grass) has been observed to contain 33 per cent. of the species found on grass heaths. Where the soil is sterile, the fields are frequently left in this condition for several years, and in such old "rotation grassland" approximately 46 per cent. of the grass-heath flora was found. *Rumex acetosella* is generally the dominant for the first few years, but it gives place to societies of *Luzula campestris*, *Agrostis vulgaris* (often very extensive), *Galium saxatile*, *Holcus mollis*, *Polytrichum* sp., and even *Nardus*; whilst weeds such as *Spergula arvensis*, *Geranium molle*, *Scleranthus annuus*, etc. disappear. *Deschampsia flexuosa* ultimately becomes dominant and forms the tussocky turf characteristic of Bunter pasture, to which the flowers of *Senecio jacobaea* sometimes give a gay appearance.

(2) Grass heath is colonising the bare ground on the sites of the conifer and deciduous plantations which had no ground flora, and invading the bracken societies left from the oakwoods: all felled within the last ten years. The subsequent changes in the vegetation are worthy of detailed consideration.

Sheepwalk, Stonehills and Annesley Forest Plantations and Barber's Wood, all situated about five miles south of Mansfield, were seen (1919) to be covered more or less completely with *Epilobium angustifolium* and *Pteridium*. The acres of brightly coloured pink flowers presented a sight most unusual in this district, and the abundance of the plant was remarkable. Unrecorded in Howitt's county Flora of 1839 (4), it has flourished (along with *Oenothera biennis*) on the colliery waste heaps for years: these, lying just to the west of the plantations, have probably been the principal centres for its distribution, for the autumnal gales would carry the innumerable seeds, perfectly adapted for wind dispersal, over a wide area. Having once established itself on the bare soil, temporary dominance is easily attained, for the rhizome extends rapidly at a depth of about 4 in. below the surface, low enough to avoid destruction by fire, such as, for example, that which occurred at the end of the dry summer of 1921. The colonisation of ruderal areas by *E. angustifolium* has attracted attention in other parts of the country, for in the *Journal of Botany*, 47, there is a note on its sudden appearance in a wood destroyed by fire in the Isle of Wight, no plants being there before, and its nearest known habitat two miles away. It also became widespread on the battlefield of the Somme, and some years ago it was conspicuous on London building sites which had been left vacant for some time after the old houses had been pulled down.

The species subsequently gives place to *Pteridium* which becomes locally dominant; that is, in situations where it previously existed as a scattered society limited by the low illumination of the plantations, and now rapidly closing up as the result of a few years' vigorous growth in the open. The fronds grow only from 1 to 2 ft. high, and there is much bare soil exposed, providing a habitat for *Rumex acetosella* and other ruderals, mosses, especially *Funaria hygrometrica*, *Polytrichum commune*, *P. piliferum*, *P. juniperinum*, and *Ceratodon purpureus*, and for the abundant seedlings and young plants of *Calluna*. Many rosette-forming Compositae and decumbent grass-heath species are spreading in from the old rides and waysides, but these are abundant only in the open and are practically absent from the bracken societies. The dominance of *Pteridium* in these situations is threatened in several ways, for its competitors are numerous. *Calluna* is abundant, even under the closed Pteridetum, having spread in from the waysides and margins of the wood, where it has long persisted. Birch seedlings too, are common, but less abundant than *Calluna*; and, finally, seedlings and nibbled "cushions" of *Ulex* and *Cytisus* occur among the bracken. It is doubtful whether any considerable part of this area will be left to develop naturally, for replanting has already begun.

In places where the late plantations had been more open, the existing

ground vegetation of *Deschampsia flexuosa* and *Pteridium* formed a closed competitive society in which the former for the most part, became dominant. Here, however, birchwood has grown up, chiefly from the stools, but also from self-sown seeds. The stool shoots, about 3 ft. high in 1915, had reached 10 ft. by 1921, and cast sufficient shade to prevent *D. flexuosa* from flowering. Unfortunately, in the dry summer of 1921, it was destroyed by fire, and in 1923 the ground was still bare.

As already described, birchwood has arisen at the north end of Annesley Forest, and becoming dominant, has displaced the grass-heath plants and ruderals which invaded the soil exposed by the felling of the plantations. In the open, the thin cakes of dry peat and the carpets of *Polytrichum* are readily colonised by *Galium saxatile*, *Rumex acetosella*, *Agrostis vulgaris*, and by *Epilobium angustifolium*, which with *Pteridium* is abundant over the southern part of the area, though there is much bare soil. A path across the forest was found to contain 36 species of Phanerogams, approximately one-half being ruderals and weeds.

E. angustifolium is much less abundant in the clearings in the Bilhaugh district, which in 1921 were replanted with larch. The principal colonist here is *Agrostis vulgaris* but the ground vegetation as a whole is very scanty, and there is a great deal of unoccupied soil, except along the margins where the oak-birch-heath ground flora existed and has probably extended, consequent upon the disappearance of the dry leaf debris and the increase in illumination.

In the five years that have elapsed since the felling of these plantations, *Deschampsia flexuosa* seems to have made relatively little progress: but without knowing the extent to which it was present in the woods before the felling, it is very difficult to say in which of its present habitats it is a new arrival. Isolated plants occasionally occur, but the marginal *D. flexuosa* society still has a fairly definite boundary on the inner side, whether it be adjacent to *Pteridium* and *Holcus mollis* or to unoccupied soil.

(3) A large area of the oak-birch-heath of Birklands really consists of well-established grass heath, a closed *Deschampsietum flexuosae*, with associated species.

(4) Grass-heath communities are abundant on the waysides, commons and warrens. It is probable and in some cases there is evidence to show that they have once borne dry oakwood. For the most part, however, the association has been established on these habitats, as at Birklands, for a long period, and is of a different type from that already described. The dominant species is *D. flexuosa* which forms a closed and almost pure society, the tussocks being as much as 9 in. high, making the habitat very difficult for less xerophytic and more delicate plants such as *Galium saxatile*, *Potentilla* spp., *Rumex acetosella*, *Agrostis canina*, and *A. vulgaris*. On the other hand, a carpet plant such as *Viola canina* and rosette plants such as species of *Carduus* and *Cirsium*. *Senecio jacobaea*, and other Compositae flourish abundantly.

Floristic Composition of the Grass-Heath Flora.

Analysis of the flora shows the association to be complex and variable in character according to the manner in which it has been formed and the relative age of the association. The accompanying table gives details of its several component communities. As an open community colonising bare soils, ruderals such as *Epilobium angustifolium* and *Rumex acetosella* predominate, and the latter species can persist through all the subsequent changes, though its frequency is gradually reduced. *Agrostis vulgaris* spreads more rapidly than any other grass, except perhaps *Holcus mollis*, which extends from its woodland, hedgerow, and scrub situations: these species dominate "pure" grass heath which is relatively young. This community is characterised also by the presence of gregarious carpet plants, *Galium saxatile*, *Luzula campestris*, *Hieracium pilosella*, *Potentilla erecta*, and *P. reptans*, which form abundant societies, often of considerable size. On the other hand, *Deschampsia flexuosa* is dominant where grass heath replaces the scrub or woodland ground flora, or where dry oakwood changes to oak-birch-heath of the type found in Sherwood. The closed Deschampsietum, unlike the open community referred to above, prevents the germination or vegetative reproduction of its competitors, and so leads to their extermination, the conspicuous exceptions being *Ulex europaeus*, *Calluna vulgaris*, *Nardus* and *Betula*.

Table showing the Successions to Grass-Heath and Heath Associations.

Increasing age.

OPEN, MUCH BARE SOIL	LESS OPEN	CLOSED
(a) On arable land (uncultivated):		
Weeds	Ruderals:	<i>Deschampsietum flexuosae</i>
Ruderals:	<i>R. acetosella</i>	(often pure consociations).
<i>R. acetosella</i>	Heath grasses:	Sub-dominant carpet and
	<i>Agrostis vulgaris</i>	rosette species:
	<i>Holcus</i> spp.	<i>Senecio jacobaea</i>
	Societies of:	
	<i>Galium saxatile</i>	
	<i>Luzula campestris</i>	
	<i>Hieracium pilosella</i>	
	<i>Potentilla</i> spp.	
	<i>Polytrichum</i> spp.	
(b) In plantations with little or no ground flora (after felling):		
Original ground flora:		
<i>Pteridium</i>	Pteridetum	
<i>Holcus mollis</i>		
Ruderals:		
<i>E. angustifolium</i>		
<i>R. acetosella</i>		
Grass heath spp.:		
<i>D. flexuosa</i>	Deschampsietum	
<i>Agrostis vulgaris</i>	Agrostetum	
<i>Galium saxatile</i>		
<i>Polytrichum</i> , etc.		
<i>Calluna vulgaris</i>	Callunetum	? Callunetum
<i>Betula pubescens</i>	Birchwood	
<i>Ulex europaeus</i>	? Ulicetum	

Table showing the Successions to Grass-Heath and Heath Associations (contd.).

(c) Scrub with Woodland ground flora:

Pteridium
Holcus mollis *Holcus societies*
Lonicera periclymenum
Teucrium scorodonia

Grass heath:

Deschampsia flexuosa *Deschampsietum flexuosae*
 Rosette and carpet plants
 often abundant
Ulex europaeus *Ulicetum*

(d) Dry oakwood (no scrub):

Pteridium
Holcus mollis
D. flexuosa *Deschampsietum* *Callunetum*
 ("Oak-birch-heath")

List of Species of the Grass-Heath Flora.

	Normal consociation (<i>Deschampsietum</i> <i>flexuosae</i>)	Waysides	Rotation grass land
<i>Achillea millefolium</i>	o.	f.	—
<i>Agropyrum caninum</i>	l.f.	—	—
<i>Agrostis canina</i>	l.a.	—	—
„ <i>vulgaris</i>	f.—a.	a.	a.—d.
<i>Aira caryophyllea</i>	o.	—	f.
„ <i>praecox</i>	o.	—	f.
<i>Anagallis arvensis</i>	—	—	l.f.
<i>Anthoxanthum odoratum</i>	—	f.	—
<i>Arenaria serpyllifolia</i>	f.	l.a.	f.
<i>Arrhenatherum avenaceum</i>	f.	f.—l.a.	o.
<i>Bellis perennis</i>	l.a.	l.a.	o.
<i>Bromus arvensis</i> var. <i>mollis</i>	—	o.	—
„ <i>sterilis</i>	—	o.	—
<i>Campanula rotundifolia</i>	o.	f.	—
<i>Capsella bursa-pastoris</i>	r.	f. (on bare soils)	o.
<i>Carduus nutans</i>	o.—f.	f.	o.
<i>Carex</i> sp. (? <i>pilulifera</i>)	o. (generally nibbled)	—	—
<i>Centaurea nigra</i> (agg.)	—	f.	—
„ <i>scabiosa</i>	—	o.—f.	—
<i>Cerastium vulgatum</i> (agg.)	o.	f.	o.
<i>Cirsium arvense</i>	o.	f.	o.
„ <i>lanceolatum</i>	o.	f.	o.
<i>Convolvulus arvensis</i>	—	—	o.
<i>Crepis virens</i>	r.	l.f. (ruderal)	—
<i>Cynosurus cristatus</i>	—	o.	—
<i>Dactylis glomerata</i>	o.	f.—a.	f.—a.
<i>Deschampsia flexuosa</i>	d.	f.—d.	o.—a.
<i>Epilobium angustifolium</i>	—	l.a. (open habitats)	—
<i>Equisetum arvense</i>	—	r.	r.
<i>Erodium cicutarium</i>	o.	l.f.	o.
<i>Euphrasia officinalis</i>	o.	—	—
<i>Festuca ovina</i>	l.a.	—	—
<i>Filago germanica</i>	—	—	l.f.
<i>Galium cruciata</i>	—	l.f.	—
„ <i>saxatile</i>	o.—l.a.	—	f.a.
„ <i>verum</i>	—	l.a.	—
„ <i>mollugo</i>	—	a.	—
<i>Geranium molle</i>	o.—f.	f.	f.—a.
<i>Hieracium boreale</i>	—	o.	—
„ <i>pilosella</i>	l.a.	l.a.	f.
<i>Holcus lanatus</i>	o.	o.	o.—f.
„ <i>mollis</i>	o.—l.a.	f.—a.	f.—a.
<i>Hordeum murinum</i>	—	o.	—
<i>Hypericum humifusum</i>	o.	—	—

List of Species of the Grass-Heath Flora (contd.).

	Normal consociation (<i>Deschampsietum flexuosae</i>)	Waysides	Rotation grass land
<i>Hypochaeris radicata</i>	f.	a.	f.—a.
<i>Lamium album</i>	—	r.	—
<i>Lathyrus pratensis</i>	—	f.	—
<i>Leontodon autumnale</i>	f.—a.	a.	f.
„ <i>hispidus</i>	o.	—	o.
<i>Lolium italicum</i>	—	r.	—
„ <i>perenne</i>	—	f.	a.
<i>Lotus corniculatus</i>	f.—a.	a.	f.
<i>Luzula campestris</i>	l.a.	l.f.—a.	l.a.
<i>Medicago lupulina</i>	f.	a.	f.—a.
<i>Myosotis arvensis</i>	o.	—	—
<i>Nardus stricta</i>	l.a.	l.a.	r.
<i>Ornithopus perpusillus</i>	l.a.	o.	f.—a.
<i>Plantago major</i>	f.	a.	f.
„ <i>media</i>	f.	—	—
„ <i>lanceolata</i>	f.	a.	f.
<i>Polygala vulgaris</i> (aggr.)	o.	—	—
<i>Polygonum aviculare</i>	o.	o.	f.
„ <i>persicaria</i>	—	—	o.
<i>Potentilla anserina</i>	—	f.	—
„ <i>erecta</i>	a.	a.	—
„ <i>reptans</i>	a.	a.	—
<i>Prunella vulgaris</i>	o.—l.f.	f.—a.	o.
<i>Pteridium aquilinum</i>	l'd.	a.	o. (spreads from the hedges)
<i>Ranunculus</i> spp.	o.	f.—a.	—
„ <i>repens</i>	—	a.	a.
<i>Rumex acetosa</i>	—	o.	—
„ <i>acetosella</i>	f.—a.	f.	a.—d.
„ <i>obtusifolius</i>	o.	f.	—
<i>Sagina nodosa</i>	o.	o.	—
„ <i>procumbens</i>	o.	l.f.	o.
<i>Scabiosa arvensis</i>	—	f.	—
<i>Scleranthus annuus</i>	—	—	l.a.
<i>Senecio jacobaea</i>	f.—l.a.	f.	o.
„ <i>sylvestris</i>	o.	o.	—
<i>Sherardia arvensis</i>	o.	—	l.a.
<i>Spergula arvensis</i>	r.	o.	l.a.
<i>Spergularia rubra</i>	o.—f.	o.	l.f.
<i>Stellaria graminea</i>	f.	f.	—
„ <i>media</i>	—	o.	—
<i>Taraxacum officinale</i>	o.	f.—a.	o.
<i>Teucrium scorodonia</i>	l.f.	—	—
<i>Thymus serpyllum</i>	l.f.	—	—
<i>Trifolium arvense</i>	l.f.	—	—
„ <i>hybridum</i>	—	o.	o.—f.
„ <i>minus</i>	f.	f.—a.	f.
„ <i>pratense</i>	f.	f.—a.	f.—a.
„ <i>procumbens</i>	r.	—	—
„ <i>repens</i>	f.	a.	f.—a.
<i>Tussilago farfara</i>	—	o.	—
<i>Verbascum thapsus</i>	r.	—	—
<i>Veronica arvensis</i>	—	—	f.
„ <i>chamaedrys</i>	l.o.	—	—
„ <i>officinalis</i>	o.	—	—
<i>Vicia hirsuta</i>	—	f.	—
„ <i>lathyroides</i>	o.	o.	—
<i>Viola canina</i>	l.a.	f.	—

Shrubs and Undershrubs not belonging to Typical Grass Heath.

	Normal consociation (<i>Deschampsietum flexuosae</i>)	Waysides
<i>Ulex europaeus</i>	l.d.	l.d.
<i>Calluna vulgaris</i>	l.a.	l.a.
<i>Erica cinerea</i>	l.f.	o.
<i>Vaccinium myrtillus</i>	—	l.a.

(4) THE HEATH FORMATION.

Edaphic Conditions.

The Bunter heaths show edaphic characters peculiar to the heath formation, namely, the formation of a thin surface peat and of a layer of moor pan. The former varies from thin flakes of undecayed bracken humus to a consolidated layer of black peat a few inches in thickness. According to Russell, "A pan is a layer of hard impermeable rock that gradually forms at the usual water level below the surface of the soil. . . . The conditions determining the formation of pan seem to be a supply of organic matter, permeability of soil, low content of soluble mineral matter, and absence of calcium carbonate. These conditions occur most frequently on light sandy soils where for some reason the water is held sufficiently near the surface" (14). All these factors apply in the case of the Bunter Sandstone, but in a large portion of the outcrop the water table lies at a considerable depth below the surface.

The soil from the south end of Rufford Forest was examined and samples obtained for analysis. There is a very dark brown peat layer about $2\frac{1}{2}$ in. in thickness, with a flaky surface, green with lichens and mosses: it dries as a hard firm mass, continuous with the soil below. In the burnt areas, the peat has for the most part been destroyed, and the soil surface shows abundant white bleached sand. At the base of the peat, there is a sharp change to the light brown coarsely-grained soil, which is usually from 5 to 8 in. in depth, but may be as little as 1 in. or less, and in places is absent altogether, for the pan layer is actually in contact with the surface peat. The pan is dark brown in colour, but not so dark as the peat, neither is it so firm, for it crumbles easily and is not much more compact than the soil. It forms a layer 2 to 9 in. in thickness with indefinite boundaries above and below. It can scarcely be considered a hard impermeable layer, being penetrated by the roots of *Calluna* and the rhizomes of *Pteridium*, the latter in some exposures being seen in the underlying subsoil, which is a deep yellowish brown, the typical colour of the sandstone. All the above soil strata give an acid reaction with potassium thiocyanate, the pan layer producing the deepest colour.

The following table shows the humus and water content (of air-dried samples) of the preceding types of soil, but it should be stated that the number of samples analysed was small, and the figures must not be taken as

showing the range of values or the averages for the heath as a whole. The comparative colour of the mineral residues is also given as affording some slight indication of the relative amounts of iron present, and the extent to which leaching has occurred: it will be noticed that the former reaches its maximum in the pan, and the latter in the soil.

Table VI. *Humus and water content of heath soils.* (Rufford Forest.)

	Water content of air-dried sample	Humus (loss on ignition)	Residue, notes on character and colour
Surface peat (6 samples)	6.12 % Range: 4.26 to 8.58	32.61 % Range: 20.19 to 45.82	Fine grained, pale yellow (3)
Soil at surface of burnt areas	1.04 %	6.67 %	Very coarse, bleached, light buff (4)
Soil at 2½ in. (below peat)	0.65 %	2.75 %	Very coarse, bleached, light buff (4)
Soil at 7 to 8 in.	0.47 %	1.88 %	Moderately fine grained, light buff (5)
Pan	2.59 %	6.37 %	Slightly coarser than the layer above, deep yellow (1)
Subsoil	1.45 %	3.87 %	Coarse, deep yellow (2)

The numbers in brackets indicate the comparative colour of the mineral residue after ignition. No. 1 being the deepest. It is necessary to repeat, however, that these values are based upon preliminary tests only, a detailed investigation being still in progress.

The extent of the area in which the pan layer is developed is not yet known. It may be seen everywhere on Rufford Forest, and also occurs on the Sheepwalk Plantation as a black band 1 to 2 in. wide, and 12 to 15 in. below the surface. An exposure near Ollerton at the south end of Birklands showed similar indications at 12 to 18 in., but the oakwood in the vicinity of the Major Oak gave no signs of a pan layer, although the soil was examined to a depth of a yard. Other likely situations were investigated. On a small heath at Lyndhurst, for example, there are from 1 to 2 in. of loose dry humus followed by 7 in. of black soil and then by the sandy and pebbly subsoil, whilst the sandgrains show that the soil is leached to all depths examined. It will be noticed that the heath here does not bear the typical "Trockentorf" of the Callunetum. Owing to the variation in depth at which the pan may occur, one must not hastily conclude that it is absent from habitats in which it is not typically developed near the surface.

Clipstone and Rufford Forests were used as a training ground for troops during the war, and are intersected with trenches, considerable quantities of subsoil having consequently been brought up to the surface.

The Oak-Birch-Heath Community.

The authors of "The Woodlands of England" (13) include amongst the wide areas covered with this type of community, the Bunter Sandstone of Notts. (e.g. parts of Sherwood Forest). The region referred to lies between the Rivers

Maun and Meden, and is occupied by dry oakwood (or oak-birchwood), grass heath (*Deschampsietum*), and true heath (*Callunetum*). As an oakwood association with a *Callunetum* ground flora, the typical oak-birch-heath does not exist, save as a mere fringe along the margins and rides, and the heath species never form a dominant or even abundant portion of the ground vegetation. As has been already described, the break-up of the oak-birch canopy lets in *Deschampsia flexuosa*, which becomes the dominant member of the ground flora, and such areas are still to be considered as belonging to dry oakwood. Again, over the greater part of the "oak-birch-heath" area, the tree layer can hardly be said to be dominant, for the oaks, birches, and occasionally pines, occurring singly or in small groups, are separated by considerable intervals of grass heath, in which *Pteridium* and *Deschampsia flexuosa* are locally dominant, according, as previously described, to the distance between the trees, or to the length of time that has elapsed since the trees disappeared. The community is better described as a well developed, and for the most part, long established grass heath, with scattered trees, than as a woodland association with a heathy ground flora. A considerable area has been planted with pine and larch, but oaks of great age and birches still remain, remnants of the older woodlands.

The Relation of Grass Heath to the Heath Association.

Calluna seedlings and young plants occur frequently in the *Deschampsietum*, but the species only becomes abundant alongside the rides of the dry oakwood and by the waysides, i.e. in situations which have been more or less "open" for a far longer period. In all probability, the grass heath of Birklands dates back to the period 1609 to 1790, when four-fifths of the trees were felled, whilst some of the rides and roads are as old as the Royal Forest of Sherwood itself. *Calluna* is abundant amongst the grass-heath plants by the Ollerton-Worksop road, but is dominant alongside numerous rides. The plants here are old, but very short and much eaten by rabbits. In places where the plantations reach the road the wire has protected the *Calluna*, which is of the usual heathy shrubby type, a contrast to the squat spreading herbaceous cushions outside.

A field situated to the east of the Sheepwalk Plantation has lain uncultivated for many years, and three types of plant community are competing for possession. *Pteridium*, representing the woodland flora, persists near the hedgerows and on a small hill from which the trees were cleared at least 50 years ago and which is too steep for cultivation. Rainwash has kept the soil bare, except near the base where *Rumex acetosella* is abundant. The greater part of the field is occupied by grass heath, consisting of a closed *Deschampsietum flexuosae* adjoining the plantation, and the "intermediate" type elsewhere, whilst at the opposite end are numerous large well-grown clumps of *Calluna*, also of long standing. Seedlings and young plants of the latter are abundant

on the bare soil all over the hill, even under the closed Pteridetum, but have not advanced very far into the grass heath, though a moderate amount of soil surface is exposed among the societies of *Holcus mollis*, *Agrostis vulgaris*, *Luzula campestris*, etc., and although *Calluna* is abundant on the ride between the field and the plantation, it has not become established in the Deschampsietum.

The evidence points to the fact that for over a century *Deschampsia flexuosa* has remained dominant in parts of Sherwood, and that the invasion of closed grass heath by Callunetum is a very slow process.

On the other hand, the colonisation of open soils by *Calluna* is frequently rapid, a matter of a few years only. Thus, in the case of Sheepwalk Plantation and Barber's Wood, the great increase of light consequent upon the felling of the trees has let *Calluna* in amongst the open Pteridetum, and now, after five or six years, young plants are abundant. The species is also locally dominant on the cuttings of the new Mansfield Railway.

Erica cinerea, *Vaccinium myrtillus*, and *Nardus stricta* are also members of this wayside and marginal heath community, and have been observed in numerous localities. *Nardus* frequently shows as flourishing societies amongst Deschampsietum, and is replacing grass heath in many places, for instance, on a hillside forming part of the Sutton golf links, where there is considerable seepage, though no extensive areas of Nardetum have as yet been found. *Nardus* has a greater rooting depth than *D. flexuosa* and the bases of its shoots are closely crowded on the rhizome, the numerous branches of which creep obliquely upwards, so that it has a greater covering capacity and a better hold on the soil.

The Heath Association.

The most extensive tracts of Callunetum in Nottinghamshire occur on the Rufford and Clipstone Forests, situated to the north-east of Mansfield, and they probably once covered all the area between the River Maun and Rainworth Water. It is quite certain that these "wastes" have been a characteristic feature of Sherwood Forest since early English times, and the absence of villages, together with the fact that a Roman road ran along the eastern boundary, is significant. The region has a small rainfall, 26–27 in. (c. 670 mm.), and the altitude varies between 476 ft. (c. 146 m.) at Ratcher Hill and about 250 ft. (c. 77 m.) along the river valleys. The water table lies nearer the surface than in the upland area further south. The replacement of woodland humus by surface peat, the pronounced leaching of the soil and the formation of pan are its edaphic characters, whilst its biotic features include the abundance of *Pteridium* and the occurrence of isolated trees such as *Betula* sp., *Crataegus* sp., *Pyrus malus*, and *Prunus spinosa*. Although, as we have seen, the invasion of dry oakwood by a heathy ground flora goes on very slowly, yet the presence of small areas of Callunetum in Birklands shows that here, at any rate, retrogression to heath is complete. The Sherwood heaths are of great age, but

the probability is that, as in the case of the New Forest heaths, they have been formed by the degeneration of dry oakwood, and are therefore not primitive.

The heath flora is very scanty, and would be still poorer were it not for the frequent fires which interfere with the dominance of *Calluna* and initiate a series of subseries, similar on the whole to those already described in the case of grass heath. The societies characteristic of the heath association are not strictly confined to this plant community, and a large percentage of the species usually listed as occurring on heaths belong to the grass-heath association. (One-half of the species listed in *Types of British Vegetation*, p. 115, are recorded also on pp. 95-96 for grass heath.) The Nottinghamshire heaths as a whole correspond with the *Calluna-Pteridium* heaths of the sandy slopes of the north-east moorlands of Yorkshire, described by Elgee (*This JOURNAL*, 2, 1914), but show a transition to wet heath in a few places.

The Heath Association comprises:

1. Areas more or less recently burnt, colonised by
 - (a) Ruderals, especially *Epilobium angustifolium* and *Rumex acetosella*.
 - (b) *Deschampsietum flexuosae*, with other grass-heath plants.
 - (c) *Pteridetum*.
2. *Callunetum* and *Ericetum cinereae*.
3. *Ulicetum europaeae*.
4. Small *Nardus-Erica tetralix* societies in moister situations.

The Burnt Areas. The ling is sometimes burnt off in March by gamekeepers, to keep the heath in good condition for pheasants, but the greatest destruction is caused during the dry summers. The peat layer is burnt as well as the vegetation, and the charred residue remains for several years, becoming gradually altered by the accumulation of bleached sand, and the spreading of fresh brown subsoil from the rabbit burrows. The year after the fire, *Pteridium* is practically the only vegetation, and owes its preservation to the depth of the rhizome in the soil. A few seedlings are present, including *Calluna*, *Rumex acetosella*, *Epilobium angustifolium*, etc., which later become abundant, though after five years there is much bare soil. *Lotus corniculatus* and *Ornithopus perpusillus* are also frequent at this stage. The ruderal societies give place to *Pteridium*, if this species was present before the fire; if not, they are succeeded by grass heath or by *Callunetum*, according to the rate at which *Deschampsia flexuosa*, *Agrostis vulgaris* and *Calluna* can colonise the soil.

The *Deschampsietum* presents no unusual features but occupies large areas of this part of the forest, with a few scattered pines, hawthorns, and birches.

Pteridetum. Where *Pteridium* is abundant, the heath presents a brownish green appearance with splashes of purple. The fronds are usually scattered and less than a foot in height, and so open that the bracken can hardly be said to have any considerable degree of dominance. *Calluna* and *Erica cinerea* are abundant throughout. *Pteridium* may be regarded as the last representative of the dry oakwood, persisting on the heath by virtue of its adaptation to

xerophytic conditions, and of its ability to escape destruction by the fires which temporarily eradicate *Calluna* and other heath plants.

Holcus mollis has practically disappeared except from areas where the bracken is high and close, as on the small heath at Lyndhurst. Here, as in north-east Yorkshire, the result of the competition between *Pteridium* and *Calluna* is largely determined by biotic factors, since the burning of the heath at regular intervals increases the frequency of bracken so that a period of temporary dominance ensues, and prevents the formation of a permanently closed Callunetum.

Callunetum.

The dominant dwarf shrub, *Calluna vulgaris*, is usually accompanied by *Erica cinerea*, though the latter is absent when the ling forms a closed association. In some parts of the heath the positions are reversed, and the apparently dominant *Calluna* is found on closer investigation to be sub-dominant in an almost continuous consociation of *Erica cinerea*. The latter, though short, forms wide spreading plants, and in addition, seedlings and young plants are exceedingly abundant, on the fresh sandy soil of the trenches as well as on the peat. *Polytrichum commune*, *P. piliferum*, *P. juniperinum*, *Webera nutans*, *Ceratodon purpureus*, *Dicranum scoparium*, *Funaria hygrometrica*, *Cladonia furcata*, *C. pyxidiata*, *C. floerkeana*, and *C. caespititia* flourish on the peat between the shrubs, but flowering plants, other than the dominant heaths, are rare. It is interesting to note the occurrence of *Plantago coronopus* on the ridges of the rides across the forest.

Nardus is a frequent member of the path and wayside flora. *Vaccinium myrtillus* flourishes by the waysides but, singularly enough, appears to be absent from the heath. *Triodia decumbens* is found occasionally, and mats of a species of *Carex* (? *C. leporina*) much attacked by rabbits.

Some small plantations of oak, beech, birch, and conifers cap the hills of the ridge that crosses Rufford Forest. Strawberry Hill bears oakwood, mainly *Quercus sessiliflora*. As might be expected in such an exposed position, the trees are slender and rather scraggy in appearance, with an average height of about 20 ft. (6 m.). The plantation is very open and attracted attention in that it is the nearest approach so far seen in Sherwood to the typical oak-birch-heath community, i.e. with *Calluna*, the dominant member of the ground flora. In this case it is obvious that the ground flora preceded the oaks, and maintaining its hold on the soil, together with *Pteridium*, now forms an anchorage for heaps of leaf debris, among which were discovered a few birch and oak seedlings (*Q. sessiliflora*)¹. *Funaria* is abundant, and it should also be stated that the pan layer occurs here at a depth of 12 in.

¹ It is clear from the progress of knowledge since *Types of British Vegetation* was published that oak-birch-heath is really a transitional successional stage between heath and oakwood, which, owing to various factors delaying or preventing the development of forest, remains in existence for long periods and thus comes to occupy large areas of sandy country.—Editor, JOURNAL OF ECOLOGY.

Rather Hill is mainly a planted birchwood, with some *Q. sessiliflora* and *Pinus sylvestris*. The birch is spreading on to the adjoining heath, but though seedlings of *Pinus* were looked for, none were found. Within the wood, *Pteridium* and *Deschampsia flexuosa* are abundant, with extensive carpets of mosses, principally *Dicranum scoparium* and *Funaria hygrometrica*, *Plagiothecium denticulatum*, *P. elegans*, *Webera nutans*, and *Dicranella heteromalla*, accompanied by the Hepatics, *Lepidozia reptans* and *Lophocolea bidentata*. *Calluna* has presumably disappeared, for this birchwood has a closer canopy than the oak plantation described above.

Ulex nanus and *U. gallii* have both been recorded as occurring on these heaths (4, 5). The former is still present on the Lyndhurst heath and various parts of Rufford Forest, growing amongst *Erica cinerea*, *Deschampsia flexuosa*, and also *Calluna*, the plants being generally of the prostrate type, and occasionally forming rabbit-nibbled clumps a foot in height. The species is a very inconspicuous element of the flora and a rapid survey may give a misleading impression of its absence from the heath.

Genista anglica occurs on the Lyndhurst heath, seedlings on the open soil with *Rumex acetosella* and *Calluna*, prostrate plants amongst *Deschampsia flexuosa*, and taller erect shrubs in flower growing up through dense *Calluna*, as in the case of *Ulex europaeus*, described later.

Ulicetum europaeae. *Ulex europaeus*, abundant by the waysides, does not form such a striking portion of the heath flora as one would expect after reading Evershed's description. It is absent from large areas of Rufford Forest. Its restricted distribution seems to be due to the extensive fires that ravage the heath and to its relatively slow rate of seed dispersal. Gamekeepers aid in its destruction, for the gorse gives better shelter to rabbits than to pheasants, and as the societies grow large they are either burnt off or entirely uprooted.

From its wayside habitats the gorse is extending across the heath at Lyndhurst, and on Rufford Forest, where in the neighbourhood of Elmsley Lodge, several interesting societies were investigated. The *Ulicetum* here has evidently succeeded *Deschampsietum*, and is adjacent to *Callunetum* with *Erica cinerea* sub-dominant, on the one hand, and to *Pteridetum* alongside. *Ulex* is spreading abundantly in the former area, but not in the latter, except where *Pteridium* is scattered and has given way to a continuous turf of *D. flexuosa*. Furthermore, the new plants appear to arise in lines radiating, like the rabbit runs, from the central clump. There may be a real relation between the two, for there seems no reason why rabbit tracks as well as footpaths, should not be utilised by ants which, according to Weiss, are chiefly responsible for the dispersal of the seeds. At Lyndhurst, owing to the attacks of rabbits, the gorse has the usual cushion form where it grows in the open or amongst *D. flexuosa*, but plants of the "erect" type arise from the centre of many well-grown shrubs of *Calluna*, where it is protected. They ultimately displace the ling and give rise to small closed societies with no ground vegetation whatever

in the centre, whilst on their margin dead and non-flowering cushions of *Calluna* are to be found.

Wet Heath.

The high degree of porosity of the Bunter Sandstone, the relatively great depth of the water table, and the prevalence of dry valleys provide the reason for the sparse development of wet heath in this region.

The Lyndhurst heath lies at the head of Foulevil Brook, a small tributary of Rainworth Water. It is intersected and bounded on the south by a hollow which, before the sinking of the mines in the Mansfield district, was usually full of water. Investigated in August, 1922, after a week of heavy rain (4.6 in.), it was even then dry throughout, except at the end, where there was a "drowned" flora including *Epilobium angustifolium*. The black soil is more than 18 in. deep, and leaching is well marked. At the higher end of the hollow, it is covered with 3 in. of humus on which the grasses *Holcus mollis* and *Agrostis vulgaris* are co-dominant, forming a resilient turf with societies of *Galium saxatile*, *Veronica chamaedrys*, *Senecio jacobaea*, and *Carex leporina*; and lower down, *Juncus conglomeratus*, *J. effusus*, *Carex* spp., *Urtica dioica*, *Rumex* spp. and *Cirsium palustre* occur, generally bordered by a zone of *Ranunculus repens* and *Polygonum amphibium*, with *Hydrocotyle vulgaris* and *Salix aurita*, whilst amongst the surrounding *Holcus* are *Euphrasia officinalis*, *Pedicularis palustris*, and *Salix repens*. At a somewhat higher level, fringing the Callunetum, is a line of *Nardus* and *D. flexuosa*, accompanied by small societies of *Erica tetralix*.

The hollow shows up as a bright green track across the purple heath, but the definite boundary formed by the old shrubs of ling is now being broken up, for with the drying up of the valley, *Calluna* is spreading downwards, preceded by grass heath.

Coxmoor is situated east of Kirkby, at the crest of the Bunter escarpment, 600 ft. (c. 180 m.) above sea-level, with an average rainfall of 30 in. (c. 850 mm.). The wood attracts attention on account of the water standing in the ditches (a rare occurrence on the Bunter); so that the ground water lies near the surface. The soil is stiffer than usual and distinctly sticky in wet weather. One-half of the plantation was felled ten years ago and the open area shows an interesting mixed ground flora of the damp oakwood type, ruderals, gregarious grass-heath species, and scrub. In addition, there are numerous large tussocks of *Molinia caerulea*, *Juncus squarrosus* societies, and alongside the ditches, *Juncus effusus*, *J. conglomeratus*, *Dryopteris thelypteris*, *Lotus major* (= *L. uliginosus*), *Deschampsia caespitosa*, *Ranunculus repens*, and *Salix caprea*. *Vaccinium myrtillus* fruits abundantly and *Nardus* is frequent on the rides.

The Coxmoor plantation is an old one, and the nature of the vegetation existing before afforestation is unknown. If not replanted, its future ecological history will be interesting.

Floristic Composition of the Heath Association.

CALLUNETUM:

<i>Calluna vulgaris</i>	d.
<i>Deschampsia flexuosa</i>	l.a.
<i>Epilobium angustifolium</i>	l.a.
<i>Erica cinerea</i>	s-d.
<i>Galium saxatile</i>	o.—f.
<i>Genista anglica</i>	r.
<i>Nardus stricta</i>	l.a.
<i>Plantago coronopus</i>	f.
<i>Polygala serpyllacea</i>	o.
<i>Pteridium aquilinum</i>	l.a.
<i>Scabiosa arvensis</i>	o.
<i>Thymus serpyllum</i>	l.f.
<i>Triodia decumbens</i>	o.
<i>Ulex europaeus</i>	l.a.
„ <i>nanus</i>	l.f.
„ <i>gallii</i>	r.
<i>Vaccinium myrtillus</i>	l.a.

and many spp. which are more characteristic of grass heath.

WET HEATH:

<i>Carex leporina</i>	l.a.
„ spp.	a.
<i>Cirsium palustre</i>	l.a.
<i>Deschampsia caespitosa</i>	l.
<i>Dryopteris thelypteris</i>	r.
<i>Eleocharis multicaulis</i>	r.
<i>Erica tetralix</i>	o.
<i>Euphrasia officinalis</i>	o.
<i>Hydrocotyle vulgaris</i>	o.
<i>Juncus conglomeratus</i>	a.
„ <i>effusus</i>	a.
„ <i>squarrosus</i>	l.a.
<i>Lotus major</i>	l.f.
<i>Molinia caerulea</i>	l.f.
<i>Nardus stricta</i>	a.
<i>Pedicularis palustris</i>	o.
<i>Polygonum amphibium</i>	l.a.
<i>Ranunculus flammula</i>	r.
„ <i>repens</i>	a.
<i>Rumex crispus</i>	f.—a
„ <i>obtusifolius</i>	f.—a.
<i>Salix aurita</i>	o.
„ <i>caprea</i>	o.
„ <i>repens</i>	l.f.
<i>Stellaria graminea</i>	f.

SUMMARY.

1. The climatic and edaphic conditions of the Bunter Sandstone are, briefly, a low rainfall, a deep coarse dry sterile soil, low lime content, a low content of soluble minerals, and a tendency to the formation of acid humus and of thin peat, accompanied by the leaching of the soil, which lead to the development of pan, involving a subsequent change in the vegetation.

2. A. THE DRY OAKWOOD CONSOCIATION includes the natural and semi-natural oakwoods of Sherwood Forest in which *Quercus robur* and *Q. sessiflora*, singly or together, are locally dominant. The woods conform to type, but the shrub layer is so poor in individuals as well as in species that it is almost non-existent, and, as a light absorbing layer, the stratum of *Pteridium* comes next to the tree canopy. The majority of the herbaceous species belong to the grass-heath association, and are abundant in open and marginal situations only. The real ground flora of the dry oakwood is scanty almost to the point of extinction, and it is shown that the absence of small geophytes and carpet plants is largely due to the slow rate of decay leading to the accumulation of loose dry humus, a factor also affecting the invasion of the oakwood by the heathy ground flora.

B. THE SCRUB ASSOCIATION occurs principally by the waysides and on the commons and warrens, where it frequently develops into a progressive Ulicetum.

C. THE GRASS-HEATH ASSOCIATION arises in various ways, chiefly by the degeneration of oakwood, and by the colonisation of the waysides and of land which is allowed to pass out of cultivation. Its most characteristic consociation

is a closed *Deschampsietum flexuosae*, which has a considerable degree of stability, but ultimately passes into heath.

3. THE HEATH FORMATION. The typical oak-birch-heath of the south of England appears to be absent from Sherwood, the succession here being rather the replacement of the oakwood ground flora by *Deschampsietum* and not directly by *Calluna* and other true heath species.

A. *The Heath Association*. Mainly represented by *Callunetum*, this occupies the extensive "wastes" of Rufford and Clipstone Forests, and is also abundant on wayside habitats. Whilst the heaths are of great age, they are not considered to be primitive, but as an edaphic succession following the degeneration of oakwood. There is no evidence of *Pinus sylvestris* spreading spontaneously in this area.

B. *The Wet Heath Association* is developed in damp hollows where the ground water lies near the surface, and is very restricted in extent.

The vegetation of the alluvial flats and river valleys has yet to be investigated.

The writer has great pleasure in expressing his obligation to the land-owners and estate agents who kindly granted free access to their woods, to Dr H. S. Holden for much invaluable advice, to Prof. J. W. Carr, of Nottingham, and Prof. McLean Thompson, of Liverpool, for the use of the university libraries, and to the Director of the Royal Botanic Gardens (Kew) and the late Mr J. A. Wheldon for help in the identification of species. He is also indebted to the British Association (Sherwood Forest Survey Committee) for a grant towards the expenses incurred during the investigation.

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- (18) **Svinnerton, H. H.** "The Bunter Sandstone of Notts. and its Influence on the Geography of the County." *58th Report Nottingham Nat. Soc.* 1909-1910.
- (19) **Tansley, A. G.** *Types of British Vegetation*. Cambridge University Press, 1911.
- (20) **Wa't, A. S.** "On the Causes of Failure of Natural Regeneration in British Oakwoods." *This JOURNAL*, 7, 1919.

NOTICES OF PUBLICATIONS ON OVERSEAS VEGETATION

SOUTH AUSTRALIA

Osborn, T. G. B. "On the Ecology of the Vegetation of Arid Australia. No. 1. Introduction and General Description of the Koonamore Reserve for the Study of the Salt Bush Flora." *Trans. Roy. Soc. S. Austr.* **49**, p. 290. Plate XXIV. 1925.

Of the total area of Australia about 37 per cent. receives 10 inches or less rain per annum and may be defined as "arid." In the state of South Australia the proportion of the arid area is as much as five-sixths. Up to the present time knowledge of the vegetation of these arid regions is almost wholly on general lines and detailed studies are few. The present paper is mainly a summary of the present knowledge of the communities of the arid regions, especially in South Australia, and of their distribution and relationships. The eucalypts so characteristic of the coastal belt disappear in the interior except along river beds and on flats liable to occasional flooding. Dwarf eucalypts (mallee) form a characteristic vegetation in the semi-arid zone with 8-10 inches of rain.

Two types of community cover most of the arid area; a "scrub" community with low growing trees, mostly species of *Acacia*, which is mostly on rocky slopes, and second, a community of "salt-bush" or "blue bush" on the plains. This is composed of species of *Atriplex*, *Rhagodia*, and of *Kochia*. These types merge into one another and there is often a broad junction belt of a mixed type. The salt bush vegetation is regarded as a distinct vegetation type characteristic of regions of 10 inches rainfall or less. As compared with other regions with a corresponding climate, these salt bush communities are remarkably luxuriant and rich, both in species and in individuals. This is due largely to the capacity of the dominant plants to absorb water through the leaf surface and so to make use of light showers which otherwise would be ineffective.

At the present time much of the vegetation of the arid regions of Australia has been more or less profoundly altered by the biological factors of grazing and rabbits introduced by the white man. In the primitive undisturbed condition, the dominating plants are in a state of delicate equilibrium with the environment. When this balance is upset far reaching changes are brought about. The regeneration of the woody plants is wholly or largely prevented and the salt bushes are killed out and destroyed by continued grazing. One result is the production of bare areas which only support a flora of annuals and are liable to excessive erosion. Such areas are of practically no value for stock.

With a view to the study of the problems of this retrogression in detail, a vegetation reserve has been established at Koonamore. This consists of 1500 acres and at present has a very degenerate vegetation. The trees and woody plants stand on ground that has little flora except annuals; the trees are not reproducing themselves. The results of observations and investigations at this reserve will be awaited with interest and should be of much value both from the ecological and economic standpoints.

R. S. A.

Osborn, T. G. B. "Notes on the Vegetation of Flinders Island. The Flora and Fauna of Nuyt's Archipelago and the Investigator Group. No. 18." *Trans. Roy. Soc. S. Austr.* **49**, p. 276. Plates XXI-XXIII. 1925.

This is a further contribution to the study of the islands off the south coast of South Australia of which earlier portions have been already noticed in this JOURNAL (**12**, p. 352, 1924).

Flinders Island is the largest of the Investigator Group and is distant 18 miles or more from the mainland. The area is about 9000 acres. Like other of the islands, it is built up of limestones overlying granite. The island has been utilised for farming operations and the human influence has considerably modified the vegetation. Burning and the introduction of sheep have been the chief factors.

The vegetation falls into five types, woodland and scrub, cliffs, sand-dunes, salt swamps, and communities of ruderals and pastureland.

1. Woodlands. These form a zone round the northern end of the island, and clumps in other parts. *Melaleuca parviflora* is the dominant and forms a dense closed community with little or no undergrowth except in openings where shrubs and undershrubs are present. No eucalypt occurred in the wood but *Eucalyptus gracilis*, a mallee, was found in a few degenerate groups associated with the remains of *Melaleuca*.

2. Cliffs. Here are included an assemblage of communities varying from pioneer colonists to practically stable types. On the more stable habitats bushes and even trees occur, *Melaleuca*, *Casuarina stricta*, *Pittosporum phillyraeoides*. These tree communities are closely allied to the woodlands. The cliff communities show variations in relation to exposure, stability of soil, and the characters of the rocks and soils.

3. Dunes. The dune succession is essentially that which occurs on the mainland of South Australia. Occasional trees of *Melaleuca parviflora* occur on the more fixed dunes and indicate the approach to the woodland climax.

4. Salt swamps. Two rather extensive areas of gypsum salt swamps occur on level plains. The dominating plant is *Arthrocnemum halocnemoides* var. *pergranulatum*. Near the margins other halophytes are present. The highest community here is a thicket of *Melaleuca halmaturorum* which is associated with several salt tolerant plants.

5. Ruderals and pasture communities. These include a varied assemblage, largely composed of plants alien to the island or often to Australia. Annual grasses are frequent. Seedlings and young plants of indigenous shrubs also occur, especially *Myoporum insulare*. This plant forms a dense scrub at the southern end of the island which is regarded as a secondary community following disturbance.

Excluding the salt swamps, the vegetation here has a clear climax in the *Melaleuca parviflora* woodland. *Casuarina stricta*, which forms a definite unit on Pearson Island, is here confined to the few granite outcrops. This is regarded as a vestigial outlier of the mainland forests at the climatic limit. The *Melaleuca forest*, however, has a different position. On the mainland it is a seral community ultimately replaced by mallee. It appears as an ultimate stage on the islands where the mallee is quite or almost absent.

In regard to the flora, 108 species were collected; a much larger number than were previously known from the island. Of this total 24 per cent. are aliens. A complete list of the flora is given with the life-forms, on Raunkiaer's system, notes on the habit and habitat, and the occurrence on the other islands visited. The spectrum of the life-forms agrees closely with that for Pearson Island and shows a close alliance with those of the arid parts of the mainland. There is a high percentage of therophytes and chamaephytes and a very low percentage of hemicryptophytes.

The paper is illustrated by three plates of photographs showing the main features of the vegetation.

R. S. A.

NEW SOUTH WALES

McLuckie, J. and Petrie, A. H. K. "An Ecological Study of the Flora of Mount Wilson. Part III. The Vegetation of the Valleys." *Proc. Linn. Soc. of New South Wales*, 51, pp. 94-113 with Plates VIII-X and 6 figures in the text. 1926.

The present paper deals with the vegetation of the valleys which frequently intersect the Mount Wilson Plateau. The *Ceratopetalum-Doryphora* Association, already noted as occurring on the basalt slopes with a south to south-east exposure, is here dealt with in regard to its occurrence in the deep river-valleys cut out of the sandstone. Its distribution is recorded as varying with the physiography of the country and an appreciation is given of its relation to adjoining types of vegetation. An interesting comparison is made of the structure and composition of this type of vegetation in its occurrence on the basaltic soil and the Hawkesbury sandstone. No marked discontinuity in the physiognomy of the type is to be noted, for the dominants are unchanged, although certain important and striking differences occur in the composition of the subordinates. On the sheltered south and south-east slopes the association continues down from the basalt caps into the bottom of the sandstone valleys. In the more exposed sandstone valleys the association is confined to the creek-bed at the bottom. The variation in the two occurrences of this type is mainly attributed to the difference in water content of the soils, which, on the sandstone, renders the dominance of *Ceratopetalum* and *Doryphora* less effective, so that more opportunity is afforded to competing species of trees. There are subsidiary and more local differentiating effects such as the lower light intensities at the base of the precipitous cliffs in the sandstone and exposure of bare rock surfaces. The general impression, gained from a study of the table illustrating the range and relative frequency of the chief constituents and the list of species with their degree of abundance, is that the full expression of the type occurs on the sandstone, and it is rather a preclimax that develops on the basalt so far as the limiting factors permit.

The discussion is illustrated by diagrammatic sketches of typical tracts of country showing the general topography and geological structure. Accompanying sketches of the same areas show, by the aid of symbols, the correlative distribution of the types of vegetation. The reduction for purposes of reproduction unfortunately makes the symbols a little difficult to recognise, but these pairs of sketches which can be superimposed in imagination, give a clear interpretation of the text and easily enable the reader to understand the discussion.

The other vegetation type of the valleys is that of the *Eucalyptus* forests, which also vary in distribution, extent and luxuriance with the aspect. They occur on the fringes of the basalt which are too exposed to be occupied by the *Ceratopetalum-Doryphora* type and on the edges of the sandstone adjacent to the basalt. Two associations and several consociations are recognised in these *Eucalyptus* forests, the dominants in each case being species of *Eucalyptus*. Their distribution and composition are also clearly shown by diagrammatic sketches of the country and lists of species.

In a short note on succession the inter-relations of each of the three climax communities of Mount Wilson are discussed, and natural changes of the habitat likely to favour one or other of the types are indicated. Such changes, however, will undoubtedly be very slow. Notes are also given on the effects of such alterations of the natural vegetation on agricultural practices.

With this Part the authors conclude their account of the primary survey of the Mount Wilson area in so far as the main plant communities are concerned. A further Part is to contain the more detailed records of the work.

T. F. C.

NEW ZEALAND

Allan, H. H. "A Remarkable New Zealand Scrub Association." *Ecology*, 7, p. 92. 1926.

The correlations of form with environmental conditions and the plasticity of many species in the New Zealand flora are well known. The scrub that is described in this paper is a remarkable exemplification of this plasticity. It occurs on a windswept coastal hill, 300 m. high, on the west coast of North Island. The original coastal forest has here been destroyed to a large extent. This scrub forms a marginal belt to a patch of dwarfed forest. The most common plant is *Metrosideros perforata*: this plant, in the forest, occurs as a creeping plant on the ground or as a root climber. Here it grows as a rounded shrub 1 m. high with a dense growth of branches. These shrubs are bound together by lianes many of which permanently retain the juvenile form of leaf. A remarkable occurrence in this scrub is *Podocarpus dacrydioides* and *P. spicatus*. Neither is typical of the coastal forest. These trees reach a height of about 1 m. and have the juvenile leaf form in the densely packed crown. Ring counts showed that trees of the same age in favourable stations would be 7-10 m. high. Shade plants, and especially ferns, occur below the trees. Most of these retain their juvenile form. This scrub is now being destroyed by cattle and is being invaded by grassland.

R. S. A.

SOUTH AFRICA

Staples, R. R. "Experiments in Veld Management." *Union. S. Afr. Dept. Agric. Sci. Bull.* 49. 1926.

The practice of burning vegetation, whether composed of grass or of bushes, is one that is very general throughout South Africa and is undoubtedly a custom of long standing. In spite of its frequency, there has been discussion on many occasions as to the value or otherwise of the practice. The present paper is a preliminary account of experiments undertaken with a view to the settlement of this question in the case of the eastern grass veld. A series of experimental plots were laid down in 1921 at Cedara in Natal on the grass veld, at an altitude of 3800 feet. The rainfall here averages 35.25 inches per annum and falls principally in the summer months, September to March.

Twelve plots were laid down in a grassland community in which *Themeda triandra* was the most important species. These plots received various forms of treatment as to burning, grazing, mowing, etc. While the plots were started in 1921, detailed observations commenced two years later, at which time the treatment of some of the plots was altered. Notes are given of the composition and seasonal aspects of the plots in 1923, but no details are supplied of the original composition at the start of the experiment. This is especially unfortunate as the control plot was burnt by lightning in June 1924.

From the preliminary study the following conclusions are reached:

1. The dominant grass, *Themeda triandra*, can withstand yearly winter burning if it is not grazed.
2. Burning is not injurious if carried out under suitable conditions, e.g. after rain.
3. Earlier grazing is got from plots periodically burned.
4. Spring or summer burning is harmful to *Themeda triandra* but does not destroy other climax grasses.
5. Weeds are favoured by burning.

6. Where neither burning nor grazing occurs, *Themeda* is replaced by *Trachypogon plumosus*, or with mowing or grazing but no burning by *Andropogon* and others.

The quadrat charts made in 1924 of the plots are reproduced. For purposes of comparison it is unfortunate that the forms of shading are not used consistently for the same plants throughout. Several photographs are also given.

R. S. A.

WEST AFRICA

Ainslie, J. R. "The Physiography of Southern Nigeria and its Effect on the Forest Flora of the Country." *Oxford Forestry Memoirs*, No. 5, Pp. 36, with 4 plates and 6 text-figures. The Clarendon Press, Oxford. 1926. Price 4s.

The Memoir is divided into three Parts, with three Appendices. The first Part gives a general account of the geography, geology and physiography of the country. The second Part is a brief summary of the chief local factors influencing plant growth, and the third Part outlines the main divisions of the vegetation and then discusses the different forest types.

Southern Nigeria is described as a vast sloping plain rising northwards gradually from the seaboard to an average height of 1200 ft. in the interior. On the east mountains to 6000 ft. occur, and elsewhere there are isolated smaller ranges and occasional precipitous hills. The basal rocks are of Archean age; marine deposits indicate submergence during Cretaceous and again in Tertiary times of the eastern part of the country and of the main valleys of the present rivers. Lateritic cementation is found on exposed sedimentary rocks generally and tropical red earths are common. The coast line is edged with deltaic muds and sands. The river system corresponds generally with the fall of the country from north to south; the Niger valley cuts the country into a western and an eastern portion, and the Cross River circles through the eastern portion before turning south.

A monsoon type of climate prevails, the rain coming with the south-west winds. Generally precipitation decreases with distance from the coastline; orographic features and also forest masses as opposed to deforested and exposed areas cause local variation. The deltas of the coast and river floods also provide local factors of importance. Inland the prevailing desiccating north-east Harmattan exercises considerable influence.

Three main physiographic divisions are recognised; the Littoral, the Plains, and the Uplands. In connection with the Littoral the mangrove swamps are discussed separately from the sand-bank areas. The Plains are a strip of coastal land behind the Littoral and some 40 miles wide. The Uplands are the hinterland, deeply cut by wide river valleys, and falling naturally into four subdivisions, the Yorubaland Uplands, the Udi Plateau, the Sonkwala Plateau, and the Oban Hills. Each of these three physiographic divisions is characterised by its own type of vegetation, which the author describes as a climatic series, differentiated mainly with regard to the degree of precipitations. Thus sand-bank scrub occupies the littoral, rain forest the plains, and deciduous forest and savannah the uplands. In each, however, a parallel edaphic series, dependent on the water content of the soil, is also to be recognised. This series, in the same sequence, is the mangrove, freshwater swamp, and fringing forest. The discussion of these types of forest and their subdivisions is given in some detail, and is considered generally under three headings, a general description of the physiognomy of the forest type with any special features, the floristic composition, and notes on the distribution.

The Littoral Forests, subdivided into Mangrove Forests and Sand-bank Forests, are similar to those generally occurring in the equatorial tropics. The Tropical Rain Forests are considered as comprising the Freshwater Swamp Forest and the Rain Forest. The former of these occurs along river flood plains and on areas subject to periodic inundation, and is an edaphic climax; the latter is the climatic climax of the country. Many families and genera are common to both these types of forest, but, on the whole the Swamps are characterised by Palmaceae, certain Leguminosae, Guttiferae and Apocynaceae. The rain forest favours areas not subject to inundation and has been sadly depleted by shifting cultivation. It contains the endemic elements of the West African closed forest and is characterised by Meliaceae, Leguminosae, Sterculiaceae, Euphorbiaceae, and Moraceae. Woody lianes are

prominent, and the physiognomy is typically that of equatorial forest. Special sub-types of forest are mentioned as providing transition areas to the heavy forest of the Cameroons and the neighbouring types to the north. Deciduous and Fringing Forests are considered as the next inland belt of forest. The Deciduous is more open, and on the whole there is a tendency to periodicity in that the trees are generally defoliated during the dry season. The floristic composition of these forests is somewhat similar to that of the Rain Forest previously mentioned, but representatives of a more xerophytic type are recorded. In fact the Deciduous type as here recognised appears to comprise a preclimax of the Rain Forest and an ecotone between closed forest and savannah. The Fringing Forest is a condition of the edaphic climax to the south, there discussed as the Freshwater Swamp Forest.

The Savannah Forest, an open woodland with a grass ground-cover or isolated trees in grassland, is encountered through the ecotone in ever-widening patches until it obtains general dominance where the precipitations do not exceed 50 inches a year, and is always subject to modification by local influences. Its floristic composition is typical of the Sudanese vegetation.

The Appendices contain the average monthly rainfall records for typical stations in Southern Nigeria, a table showing the occurrence and distribution of the commoner species through the forest types; and a list of the authors consulted.

Mr Ainslie is to be congratulated on providing this appreciation of the forest types of Southern Nigeria and the factors influencing them. The area under consideration is vast, and it has been no mean task to visualise this mass of vegetation and resolve it into its chief component types with their characteristic features and composition. T. F. C.

NEW BOOKS RECEIVED

Haviland, Maud D. *Forest, Steppe and Tundra: Studies in Animal Environment.* $8\frac{3}{4} \times 5\frac{1}{2}$ in. Pp. 218. Eight photographic plates, 8 text-figures and a folding map. Cambridge Univ. Press, 1926. Price 12s. 6d.

The author (Mrs H. H. Brindley) who has travelled widely in eastern Europe, Siberia and Guiana, and is already known for her contributions to ornithology and entomology, writes pleasantly and interestingly on the Guiana Rain Forest, the South Russian Steppe, the Eurasian Tundra, and (very briefly but very well) on the Siberian Taiga (northern coniferous forest). Mrs Brindley is a true naturalist, and her numerous personal observations as well as her references to those of other travellers, together with good discussions of particular types of environment, make an attractive whole. She has an excellent grasp of the conditions of life of both plants and animals in the regions she has visited, as well as a marked power of appreciation and expression of the varied beauty of scenery and atmosphere.

Stamp, L. Dudley. *The Vegetation of Burma from an Ecological Standpoint.* 10×8 in. Pp. vi + 58 and two unpagged indices. 28 photographic plates. (University of Rangoon Research Monograph No. 1.) Calcutta: Thacker, Spink & Co., 1925.

The author states in the preface that this work has grown out of a paper dealing with the Ecology of part of the Dry Belt of Burma published in this JOURNAL, 11, 1923. Its appearance in the present enlarged form with plates (illustrating the vegetation types)

is mainly due to the interest of the officers of the Indian Forest Service in Burma. The work, which is concise and systematic, will be of great value for reference both to foresters and students of vegetation.

Naturalist's Guide to the Americas. Prepared by the Committee of the Ecological Society of America on the Preservation of Natural Conditions. Assembled and edited by the Chairman, VICTOR E. SHELFORD. 9×6 in. Pp. xv + 761. 16 plates and figures. Baltimore: The Williams and Wilkins Company; London: Bailliere, Tindall and Cox, 1926. Price 45s.

This book grew naturally out of the effort to classify the existing American "nature reserves" and to indicate fresh areas for preservation. It consists mainly of concise descriptions, by many different authors, of the biota of natural regions of North America, Central America, the West Indian islands, the northern portion of South America, and the Philippines. To this are prefixed useful chapters on the "Uses, Values and Management of Natural Areas," and on the "Original Biota of the Americas North of the Amazon." One of the main impressions gained by the compilers and by the Editor, Prof. Shelford, was that of the fragmentariness of our knowledge, and especially of our almost complete ignorance of the ecology of the invertebrate land fauna. In spite of the lacunae and other inevitable defects, the work, which has involved an enormous amount of devoted labour, will certainly be of great value for reference, and should serve as a stimulus to new ecological studies and investigations of all kinds. It may be considered as a sort of provisional encyclopædia to the American biota.

Wissler, Clark. *The Relation of Nature to Man in Aboriginal America.* $8\frac{3}{4} \times 5\frac{1}{2}$ in. Pp. xx + 248. 51 text figures. Oxford Univ. Press, American Branch, New York, 1926. Price \$3.50.

This book by the Curator-in-Chief of the Department of Anthropology, American Museum of Natural History, and Professor of Anthropology in Yale University, deals with the geographical distribution of a large number of social and somatic characteristics and of traits of natural culture of various tribes of North American Indians. He finds that all these are distributed zonally from certain centres, the tribes at any given centre having the largest number of elements in a culture-complex, and those in successive surrounding zones progressively fewer. This is explained by supposing that the "trait complex" originated in the centre with few elements which gradually spread outwards in all directions (unless, of course, geographical barriers stopped them) while the centre evolved additional or more elaborate elements, which in their turn spread outwards. Thus the nucleus of the culture would come to possess its richest and most highly specialised form, while the margins only attained the primitive stage, including the elements common to the whole. The conditioning factor of this process of evolution and diffusion is the natural ecological area, where the conditions of life are favourable to the development of the culture. An outstanding example is the bison area of the Great Plains with its dominant buffalo-grass and great herds of bison, on the hunting of which the characteristic Indian culture, which here found its centre, depended.

Russell, E. J. *Plant Nutrition and Crop Production.* $8\frac{3}{4} \times 5\frac{3}{4}$ in. Pp. ix + 115. 21 photographic plates and 37 text-figures. University of California Press (Cambridge Univ. Press), 1926. Price 12s. 6d.

Sir John Russell's Hitchcock lectures at the University of California (1924) present in a short space and in the author's well known clear and attractive style an exposition of the

essentials of our knowledge of this rapidly developing subject up to the date at which they were delivered.

Spitsbergen Papers. Volume I. Scientific Results of the First Oxford University Expedition to Spitzbergen (1921). Oxford Univ. Press, 1925. Price 30s.

This is a collection of 32 papers reprinted from various scientific journals (including two from this JOURNAL) without change and bound together, with an appendix containing a list of Polyzoa, Tunicata and Hydroida collected by the expedition, and a short preface. The preface contains the following remarks (p. v). "No longer is the biological success of an expedition estimated chiefly by the number of species or genera 'new to science' which it discovers. The ecological point of view has become prominent, and the study of the interrelations of organisms in nature has become recognized as increasingly important for the proper understanding of the problems of biology." "In this respect the Arctic lands occupy a special position. Ecological detail is here reduced to a minimum. So few species are present that it becomes possible for us to master the sum of their interactions with each other and with their environment, and so to see the ecological web as a whole; and the light thus gained may be profitably applied to the greater complexity of more genial climates."

Hayek, August. *Allgemeine Pflanzengeographie*. 10 × 6½ in. Pp. viii + 409. 5 text-figures and 2 folding maps. Berlin: Gebrüder Borntraeger, 1926. Price 18 marks (paper cover).

This general text-book, covering the field of both ecological and floristic plant geography, clearly and pleasantly written, is for the most part a competent production. It is however in the floristic section that the author is most at home. The ecological section is rather superficial in parts. The account of soils is poor and scarcely up to date, of succession extremely meagre. On the other hand, a good though uncritical description is given of the ideas of the Upsala and Zürich schools. The bibliography is long, but a good deal of important work, especially American work, is omitted, and it contains many misspellings of names.

Shaw, Sir Napier. *Manual of Meteorology*. Vol. I. *Meteorology in History*. 10½ × 7 inches. Pp. xx + 339, with 121 figures. Cambridge University Press. 1926. Price 30s.

This is the first, historical, volume of Sir Napier Shaw's great manual, of which Volume IV (Part IV), "The Relation of the Wind to the Distribution of Barometric Pressure," has already been published. Volume II, "Comparative Meteorology," is now in the press. The parts of most immediate interest to ecologists are Chapter II, which deals with the Mediterranean climate as recorded by classical writers and also as analysed by modern methods, and Chapter VI, on the Variability of Mediterranean Climates in Historical Times, which cites some of the evidence, and the opinions of the authorities, for progressive and fluctuating climatic changes in this region. The author concludes that the Mediterranean climate as a whole has not altered its essential character, though there is good evidence for desiccation in the parts of Asia to the east of the Levant. The author calls attention to two factors, besides climatic changes, which may be considered meteorological, which are irreversible, and against which, in the long run, humanity is powerless, viz. the covering of fertile regions by blown sand, and the removal of upland soil to the sea by the action of rainwash and rivers. The volume is written in Sir Napier Shaw's scholarly and attractive manner, and is beautifully produced.

BRITISH ECOLOGICAL SOCIETY

SOIRÉE AT UNIVERSITY COLLEGE, LONDON

The members and guests were entertained by the President and Council at a Soirée in the Botanical Department of University College, London, at 8.30 p.m., on January 7th, at which a number of extremely interesting exhibits were shown.

In the Elementary Laboratory the President exhibited a series of photographs and specimens illustrating the history of the peat in the Pennines, showing that the forests that formerly clothed what is now moorland flourished during the latter part of the Palaeolithic age and probably degenerated during the Neolithic period.

Mr N. Y. Sandwith (Royal Botanic Gardens, Kew) exhibited a striking series of cushion plants and spiny xeromorphs from the Andes; these included the remarkable *Viola volcanica* Gill and Hook., with its rosette-like habit, *Verbena patagonica* Speg., suggestive of a *Raoulia*, *Verbena Comberi* Sandwith, like a small gorse bush, species of *Nassauvia*, *Nastanthus*, etc.

Mr V. S. Summerhayes (R.B.G. Kew) exhibited a series of Australian plants, chiefly Leguminosae, Proteaceae, Myrtaceae, Rutaceae and Compositae, showing homologous and analogous homoplasy. The *Epacris* type of foliage was represented in *Epacris* itself, in *Acacia horridula*, *Daviesia squarrosa* and *Melaleuca styphelioides*. The branched spines of *Jacksonia spinosa*, recalling *Colletia*, were strikingly paralleled by the spiny compound leaves of *Grevillea teretifolia* and *Pterophila sessilis*, while the ericoid and switch habit were illustrated in a great variety of species.

Prof. Ruggles Gates showed a series of tundra lichens collected at Murmansk (Arctic Russia).

A series of photographs by Prof. Cockayne illustrated the history of Tussock grasslands in New Zealand.

Mr S. K. Mukerji showed specimens illustrating Indian maritime and Himalayan plants.

In the Advanced Laboratory Prof. Oliver showed a series of photographs illustrating the colonisation of the Far Point at Blakeney by *Psamma* (*Ammophila*) and *Triticum* (*Agropyrum*) *junceum*, also a series of specimens showing the winter phase of a number of maritime species. The dune annuals are winter annuals, whilst those of the salt marsh are summer annuals. The perennials show varying degrees of winter greenness.

Mr W. B. Turrill exhibited a series of specimens from the Balkans, showing the application of Raunkiaer's system of life forms. The area has a low proportion of trees and shrubs and a high percentage of annuals and geophytes. The Director of Kew exhibited photographs of transplantation experiments in U.S.A. A series of growing plants of various species of *Crocus* was exhibited by Dr E. J. Collins.

Mr T. A. Dymes exhibited a number of specimens showing the modes of seed dispersal in various British flowering plants. These included *Allium ursinum*, *Asarum europaeum*, *Carex ornithopoda*, *Alchemilla vulgaris* and *Helleborus foetidus*, for which ants function as agents of dispersal, and *Arum maculatum*, for which worms perform the same function. In *Frankenia laevis* the capsule drops unopened and dehisces when wet. Other cases of "negative hygroscopicity" illustrated were *Arnoseris pusilla* and *Prunella vulgaris*.

Mr Marsden-Jones exhibited specimens of the wild *Beta vulgaris* grown in garden soil, and a putative cross with the garden beet. A fine series of specimens from maritime habitats in Portugal was shown by Prof. Oliver.

Prof. Boycott showed specimens illustrating the habitats and mode of dispersal of some freshwater snails. The young of various species of *Planorbis* were shown for comparison, those of *P. corneus* which are thick are distributed with difficulty, but the very flat shells of *P. spirorbis* adhere readily to the wet plumage of water birds.

During the evening short talks were given by Dr A. W. Hill on "Some American Trees," and by Dr E. J. Salisbury on "Some disappearing British plants."

THE ANNUAL MEETING

The Annual Meeting was held on January 8th in the Botanical Department, University College, London, at 10.30 a.m.

The President occupied the chair and there was a large attendance.

The minutes of the previous meeting were, in view of the rather long programme, taken as read. The Hon. Secretary then read his report for 1926, which was adopted.

HON. SECRETARY'S REPORT FOR THE YEAR 1926

During the past year three meetings have been held. The Annual Meeting took place in the Botanical Department of the University of Manchester on January 9th and was preceded by a Soirée on the evening of the 8th. On the 10th Prof. Weiss and the Curator conducted the members round the Cactus House and demonstrated the chief points of interest. The Society is greatly indebted to Prof. Weiss and his staff for their hospitality and the excellent arrangements, which contributed in no small measure to the success of the meeting.

Two field meetings were held. The first was on March 13th, under the guidance of Mr Sherrin, when the Bryophytic flora of calcareous soils was examined at Boxhill, and the second was on October 9th, when, under the guidance of Mr Ramsbottom, the Society examined the Fungi of the same area in conjunction with the British Mycological Society. An extended field meeting to last a week was arranged for in the neighbourhood of Exeter during August, but unfortunately the number of names sent in did not justify keeping open the hostel where arrangements had been made for the accommodation of members, and the meeting had to be abandoned. Our thanks are due to Mr Sager for making the local arrangements, and none the less because his efforts were in vain.

Two numbers of the JOURNAL have been issued during the year, in February and August, together comprising 360 pages and ten plates.

During the past year five members have tendered their resignations and we have to mourn the loss by death of Mr C. Hunter of Bristol University. We start the new year however with thirty-five new members, amongst whom we are especially glad to welcome fifteen of our colleagues in the United States, and three from Soviet Russia.

The Council's nominees for the officers and Council were elected as follows:

Vice-President: Prof. FRITCH.

Council: Dr BURT DAVY, Dr W. WATSON.

Hon. Editor: Mr TANSLEY.

Hon. Sec.: Dr E. J. SALISBURY.

The President then delivered his Presidential Address "On the History of the Vegetation of the Southern Pennines," a full report of which will appear in the JOURNAL. On the motion of Prof. Weiss, seconded by Prof. Fritch, a vote of thanks was unanimously accorded to the President for his Address.

Prof. Oliver then gave an account, illustrated by lantern slides, of certain aspects of Portuguese vegetation. He emphasised the richness of the Flora, which not only includes some 3000 native flowering plants but also a large number of aliens, particularly from S. America. The dune vegetation does not form a continuous turf but consists of numerous closely approximated bushes of *Corema alba* and other shrubby species, between which biennials and annuals form an incomplete covering; this absence of continuous vegetation is correlated with a very coarse-textured sand. The salt marsh vegetation of *Spartina stricta*, and the "Matto" with shrubby vegetation, in which *Cistus ladaniferus* is a conspicuous feature, were also described.

The meeting then adjourned for lunch in the College Refectory.

On resuming, the Hon. Treasurer presented the accounts, which were adopted, subject to audit. The year's working showed a balance of £28. 18s. 3d.

On the motion of Prof. Thoday, Mr Robert Paulson was re-elected Honorary Auditor for 1927.

The Hon. Treasurer drew attention to the fact that the satisfactory position of the Society financially was due in no small measure to the fact that the JOURNAL, which was our chief item of expenditure, was produced as economically as possible consistently with its high standard of production by the Cambridge University Press. This was largely due to the efforts of the Hon. Editor; an appreciation which the members present heartily endorsed.

Mr Tansley pointed out that the cost of the JOURNAL was much more nearly covered by subscriptions and sales of the current volume than was the case last year. This indicated a healthier financial condition than was apparent from superficial comparison of figures.

At the suggestion of the Hon. Treasurer, the President proposed that the Society should contribute a sum of £10 towards the Centenary Fund of University College, London, as a token of the Society's appreciation of the hospitality that they had there so frequently enjoyed. This was carried unanimously, and the action of the Society was appreciatively acknowledged by Prof. Oliver.

Prof. Fritch then gave an account of further work on the vegetation of Hindhead Common with particular reference to the effects of burning. The selective action due to more or less protection of the crown appeared to be chiefly operative in areas of low growth and valley areas. High growth and areas occupying exposed ridges usually showed a very high mortality, probably due to the greater heat during burning. The apparent stimulation of *Pteridium* after burning was also emphasised. In the discussion which followed Mr Tansley, Dr Salisbury, Prof. Yapp and Prof. Weiss took part.

Dr A. W. Hill (Director of the Royal Botanic Gardens, Kew) then opened a discussion on transplantation experiments, suggesting the desirability of undertaking experiments in this country similar to those carried out by Dr Hall in California, with a view to discovering whether the changes produced, if any, were of a permanent or temporary character and in what this change consists.

After a discussion, in which Dr Salisbury, Prof. Oliver, Prof. Weiss, Prof. Yapp, Mr Tansley and Mr Ramsbottom took part, it was agreed that a committee should be appointed by the Council to consider the matter in consultation with Dr A. W. Hill.

Prof. Yapp then dealt with size as a factor in plant succession, emphasizing the generally increasing size of the dominants from the pioneer phase to that of the climax and adumbrating the possible causes of this sequence and its irregularities.

Prof. Boycott described experiments on the habitats of certain freshwater mollusca in which he showed that the gill-breathing operculate snails are absent from ponds because of the unsuitability of the habitat, transplanted specimens failing to survive more than two or three years. The absence of *Planorbis corneus* from ponds was shown, on the other hand, to be due to inefficient dispersal; an outcome of the thickness of the shell in comparison with its diameter even in the young state, so that the snail would not adhere to fragments of waterweed transplanted by birds. Other more flattened species of *Planorbis* were widely distributed in the ponds studied since they readily adhere to the plumage of birds or to water weeds which the birds carry. Transplantation of *P. corneus* to ponds from which it was absent almost always resulted in successful establishment.

The meeting then concluded and the members were entertained to tea in the Research Room.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR 1926

<i>Income</i>		<i>Expenditure</i>	
	£ s. d.		£ s. d.
Subscriptions received including Arrears	214 2 8	Working Expenses:	
Less Prepayments for 1927	14 5 0	Postages	6 1 11
		Printing	5 12 10
Interest on Investment	...	Travelling Expenses (Meetings)	3 7 11
Interest on Bank Deposit	...	Bank Charges	12 0
Sales of Reprints	...		
<i>Journal of Ecology</i> —Sales, etc.:		Soirée Expenses	15 14 8
Current Volume, No. xiv, 1926	381 19 6	Clerical Assistance (Secretary)	3 0 4
Back Volumes and Parts	90 9 11		10 0 0
Advertisements	3 10 8	Paper, Printing and Illustrations	547 1 2
Contributions towards cost of Plates	...	Binding	7 0 4
(University of Birmingham and University of Alberta)	9 10 0	Postages, etc.	24 2 6
		Insurance of Stock	2 3 8
		Publishers' Commission	61 5 2
	485 10 1		641 12 10
			670 7 10
		Balance—Surplus for Year earned to	
		Balance Sheet	28 18 3
			699 6 1

BALANCE SHEET AT 31ST DECEMBER, 1926

<i>Liabilities</i>		<i>Assets</i>	
	£ s. d.		£ s. d.
Subscriptions prepaid for 1927	...	Westminster Bank—Credit Balances:	
General Revenue Account—Balances	...	Current Account	30 9 2
Surplus at 31st December, 1925	240 19 5	Deposit Account	50 0 0
Surplus from Revenue Account, 1926	28 18 3		
		Investment: £200 5 p.c. War Loan (1927–1947) at cost	80 9 2
		NOTE. A further asset is the unsold stock of the <i>Journal of Ecology</i> held for the Society by the Publishers.	203 13 6
			284 2 8

January 8th, 1927.

SUBJECT TO AUDIT

HUGH BOYD WATT,

Hon. Treasurer.

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DISTRIBUTION OF VEGETATION ON THE PLAINS OF EUROPEAN RUSSIA¹

By BORIS A. KELLER.

Professor at the Agricultural College, Vorónezh.

(With Plates II–VIII, Eight Maps and a Figure in the Text.)

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INTRODUCTION. THE CHIEF TYPES OF VEGETATION.

The climatic zonal distribution of soils and vegetation is very well marked on the extensive plains of eastern Europe, western Asia and Turkestan, expressing itself in the following sequence from north to south:

1. *Tundra*.
2. *Taiga*, i.e. Coniferous Forest with the *Podsol*² type of soil.
3. *Grass Steppe*, with Black Soil (*Chernozëm*).
4. *Semi-desert*, with Chestnut and Brown Soil (*Burozëm*).
5. *Desert*, with Grey Soil (*Serozëm*) or Light coloured Soil (*Svetlozëm*).

¹ Freely translated from the German by the Editor; proofs revised by the author. The Editor acknowledges the kind help of Dr E. H. Minns, F.B.A., of Pembroke College, Cambridge, in the transiteration of Russian names and terms.

² *Podzól* (Russian *pod*, under, and *zolá*, ash) is more correct, but *podsol* is now practically stabilised in English.

The last named is confined to the Asiatic region (Turkestan). Besides these main zones transitional zones must be distinguished, viz. *Forest-tundra* between (1) and (2), and *Forest-steppe* between (2) and (3). The fundamental cause of the zonation is change in the climatic factors—the zonal distribution of climate. But complication is introduced because the climate changes not only from north to south but also from west to east, from the oceanic climate of western Europe to the strongly continental climate of the centre of the great Eurasian continent. Again the climatic effects vary according to the various topography and the varying “rock” of different localities within each zone. The general features of the zonation correspond well with the scheme of Brockmann-Jerosch and Rübel¹, though each zone displays whole complexes of vegetation according to the local variations of conditions.

The most important historico-geological factors are first the great glaciers which formerly covered most of the plains to be described, and secondly the waters of the Caspian Basin which at one time spread over much of the south-east. For the sake of simplicity the plains may be divided into two regions with respect to the effect of glaciation. The northern forest-covered region shows the typical moraine landscape, the southern steppe region is on the whole flat, but more or less cut up by ravines. The former is mainly covered by coarse material brought by the ice, the latter shows the influence of water set free by the melting of the edges of the ice sheet.

With the disappearance of the ice and the retreat of the waters of the Caspian Basin enormous areas were thrown open to colonisation by vegetation. In this vegetation we may distinguish certain elements whose areas of distribution even to-day bear witness to their post-glacial lines of immigration. The most important are the following:

(a) *Tundra vegetation*, which may be supposed to have first occupied the ground as the ice retreated.

(b) *Coniferous forest*. The development of this was determined by the advance of the two leading coniferous species, *Picea excelsa* and *Pinus silvestris*. The communities which they form show to a considerable extent a combination of tundra and forest vegetation.

(c) *Deciduous forest*. The mid-European broad-leaved deciduous forest, represented in Russia by oak forest, clearly shows a gradual impoverishment and dying out from west to east, and does not extend beyond the Urals.

(d) *Herb and grass vegetation of the steppes*. This on the contrary represents a stream passing from east to west. On the plains of Russia the flora of the distant steppes of the Altai is strongly represented, and the westward stream of steppe plants at one time reached even to southern Sweden and England, where certain species still linger.

(e) *The typical flora of the semi-deserts and deserts* has its origin in the great mountain and desert species-forming laboratory of Turkestan.

¹ *Die Einteilung der Pflanzengesellschaften*, 1912, p. 67.

In southern Russia, beyond the limit of distribution of erratic blocks, rare species occur which may be taken as relicts of the Ice Age and partly even of preglacial Tertiary times; and in various deposits of peat and lignite in middle and south Russia, belonging to interglacial and preglacial times, interesting plant fossils occur. But data for the reconstruction of the history of vegetation from the Tertiary to the present time are still very scanty.

At Kíev, at Mezino (Gov. Chernígov); at Kóstenki (Gov. Vorónezh), etc., palaeolithic remains occur, going back to the Aurignacian. These palaeolithic men, contemporary with the fauna and flora of the Ice Age, were acquainted with the use of fire, and their history is interwoven with that of the vegetation from a very early period.

In the following brief sketch of the vegetation it will only be possible to touch lightly on the enormous mass of data accumulated by Russian plant geographers, pedologists and foresters. The sketch maps (between pp. 192 and 201) will, it is hoped, enable the reader more easily to form a picture of the distribution of the factors and of the vegetation.

I. TUNDRA AND FOREST-TUNDRA.

Pohle (1903) distinguishes Tundra and Forest-tundra as two zones, the arctic and the subarctic.

Tundra. To this belongs only the extreme north-east—the two islands of Nówaya Zemlyá, the island of Vaigách, and the Paikhoy mountains and surrounding country. The most characteristic trait of this region is that there is no closed covering of flowering plants, though many species are present. The whole country between pure tundra and the zone of closed forest belongs to the subarctic zone or forest-tundra, and here most of the plant communities are closed. In this zone the tundra vegetation is represented mainly by various peat-forming communities. “Peat-hillock tundra” has a special distribution and on this Pohle comments that the alternation of peat ridges, poor in species of *Sphagnum*, with water channels, whose vegetation consists mainly of *Sphagnum*, gives the physiographical character of the tundra moors. These are only found in the subarctic region, i.e. the transition region between boreal forest and arctic desert. In fact the peat ridges represent the arctic element, while the channels are to be considered as the remains of the *Sphagnum* bogs of the northern forest region. According to Pohle’s description the peat *ridges* remain frozen even in summer close to the surface, and the surface itself is sometimes nearly bare of vegetation over great stretches.

Rubus chamaemorus is especially characteristic of the peat ridges. The woody plants of these ridges nearly all creep on the ground and only exceptionally rise a foot above it. The other most important dwarf shrubs are:

Salix glauca
Betula nana
Arctous (*Arctostaphylos*)
alpina

Ledum palustre
Empetrum nigrum
Vaccinium uliginosum
V. vitis-idaea

Andromeda polifolia
Lyonia (*Cassandra*) *calyculata*

The most important herbs are:

<i>Tridentalis europaea</i>	<i>Bartsia alpina</i>	<i>Deschampsia caespitosa</i>
<i>Polygonum viviparum</i>	<i>Festuca ovina</i>	<i>Juncus trifidus</i>
<i>Pedicularis lapponica</i>	<i>Eriophorum vaginatum</i>	

The phanerogamic vegetation is not closed.

The hollows between the peat hillocks are covered with water to a greater or lesser degree and have the character of Sphagnum bog. Pohle never found ice in summer even at a depth of 1.6 m. in the dead *Sphagnum* of the hollows. The phanerogams are typical Sphagnum-bog plants and other bog herbs:

<i>Andromeda polifolia</i>	<i>Carex rotundata</i>	<i>Comarum palustre</i>
<i>Oxycoccus palustris</i>	<i>C. rariflora</i>	<i>Hippuris vulgaris</i>
<i>Drosera rotundifolia</i>	<i>Menyanthes trifoliata</i>	<i>Equisetum heleocharis</i>
<i>Eriophorum russeolum</i>	<i>Caltha palustris</i>	

Tanfil'ev describes the following characters of the hillocks. Diameter 5–25 m., height about 3–5 m. The main mass of the hillock consists of *Sphagnum fuscum*. The surface has a dirty white or grey colour derived from the lichens: *Cladonia rangiferina*, *Cetraria nivalis*, *Stereocaulon paschale*, *Cornicularia aculeata*, *Sphaerocarpon fastigiatum*: also *Ochrolechia tartarea* on mosses. Of these latter mainly *Sph. fuscum* and *Polytrichum strictum*.

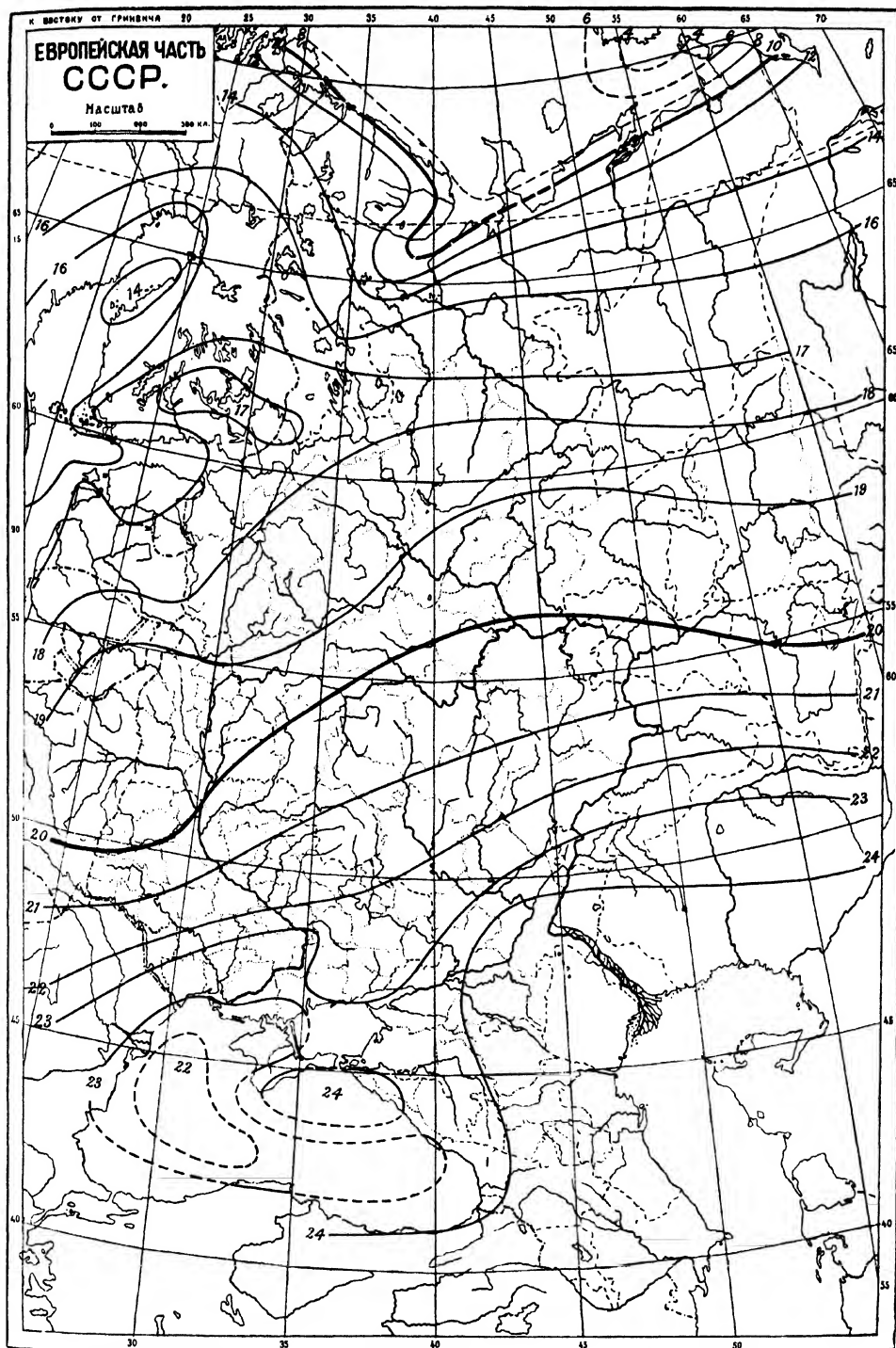
Tanfil'ev made diggings in the peat of the hillocks down to the mineral substratum and both on this underlying sand or clay and also in natural sections of the peat he found remains of birches and spruces. Pohle observed the same thing. The former author considered that these tree remains resulted from the destruction of the forest edge by growth of the Sphagnum bog and the formation of permanent ice in the moss soil. The hillocks themselves he regarded as a peculiar kind of Hochmoor. Pohle thinks that this advance of tundra on forest was largely helped by human destruction of the trees. The forest stretched much further northwards in postglacial times when the climate was warmer than it is now. But later the islands of forest were easily suppressed by the better adapted tundra communities.

The tundra moor is the most important community which alternates with forest. In addition there are arctic heath, and moss and lichen tundra of various types, *Saliceta*, occasional meadows, and communities of halophytes on the sea shore.

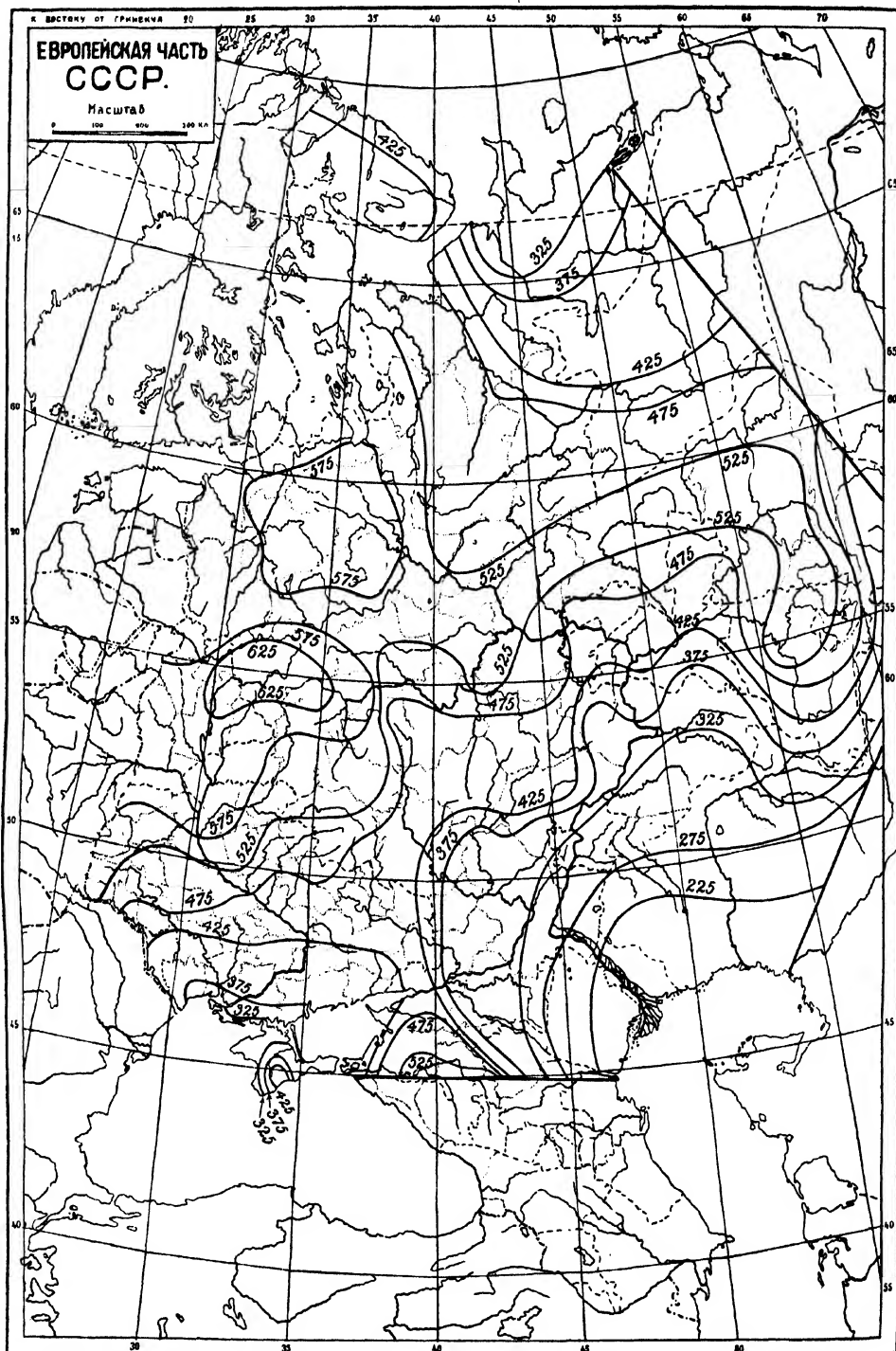
Of trees *Picea* and *Betula* play the leading rôle on the northern tree limit, in the east *Larix sibirica* as well. Besides these Pohle cites for the Kanin peninsula:

<i>Populus tremula</i>	<i>Sorbus aucuparia</i>	<i>Salix caprea</i>
<i>Prunus padus</i>	<i>Alnus incana</i>	<i>Pinus silvestris</i>

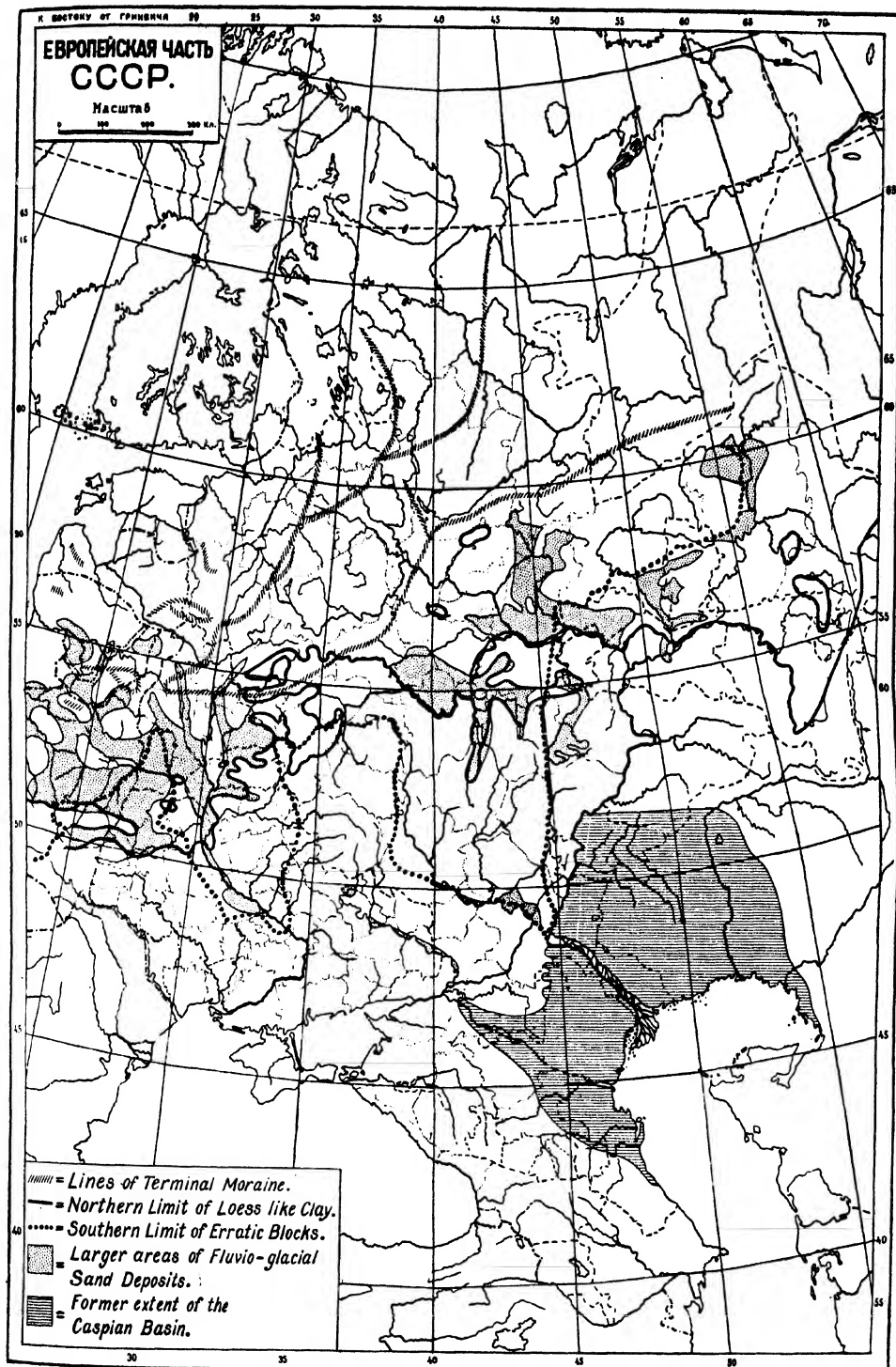
The extreme northern forms of *Picea* and *Betula* have been little investigated. The spruces belong to *Picea excelsa* Link and *P. obovata* Ledb. which are connected by transitional forms. Of the birches there is a series of forms which may be united under *Betula tortuosa* Koehn.—also *B. pubescens* and to some extent *B. verrucosa*.



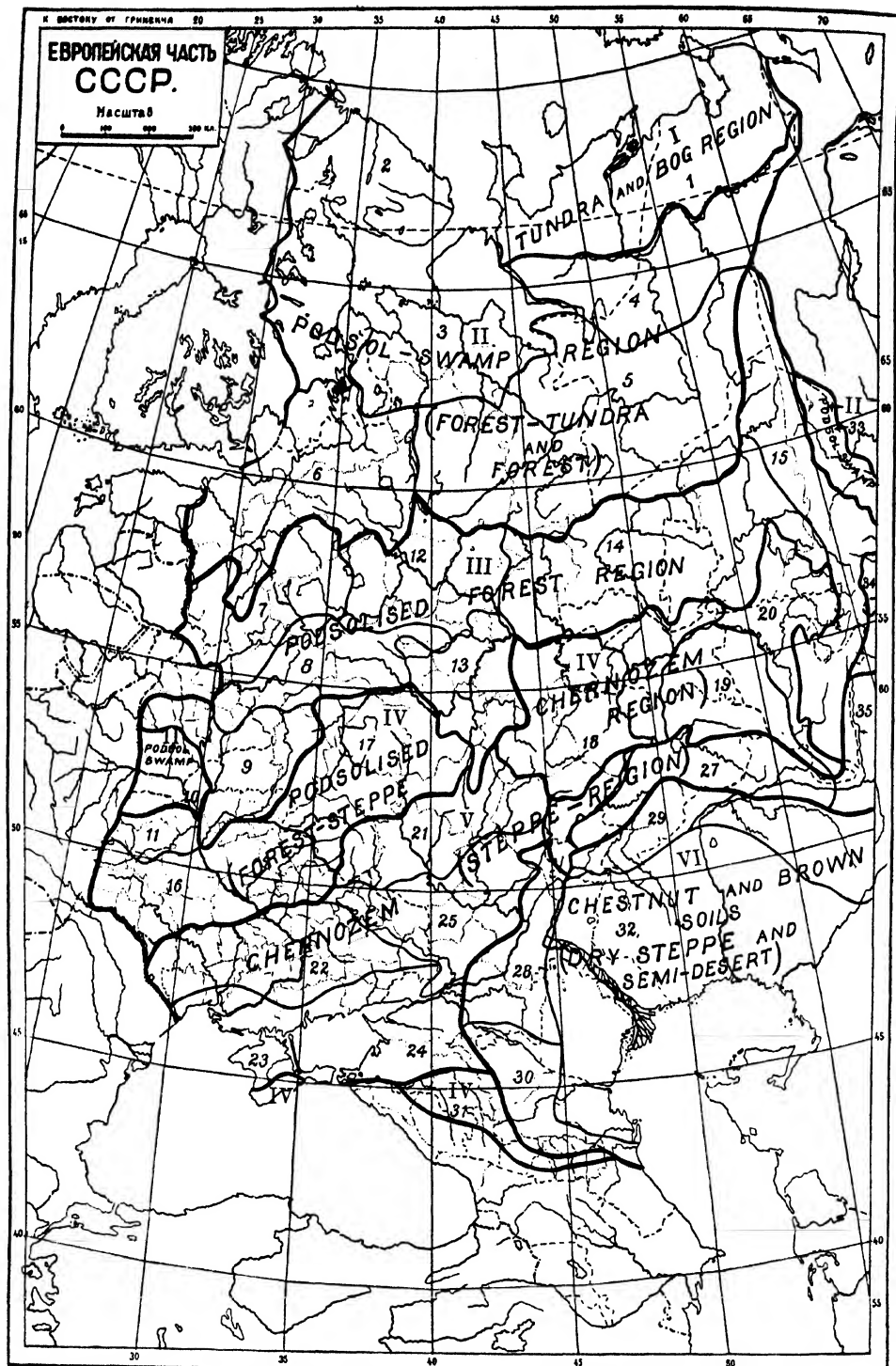
МАР 3. July Isotherms (air-temperatures in °C.). (From the Climatological Atlas of the Chief Physical Observatory, Petersburg, 1900.)



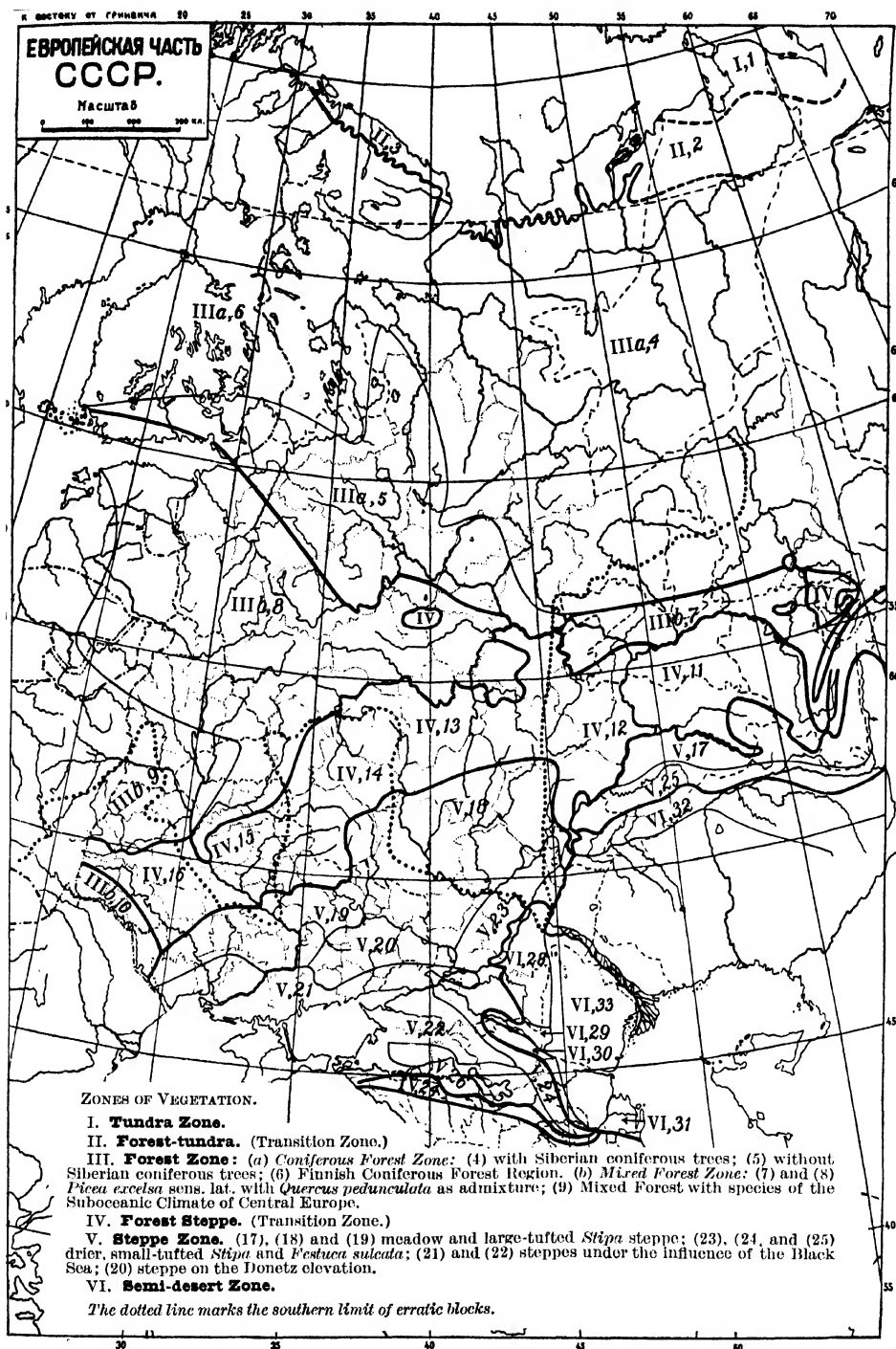
MAP 4. Mean annual precipitation (mm.). (From S. Nebolsin, Atlas of Maps of the mean distribution of atmospheric precipitation in European Russia, Petrograd, 1916.)



MAP 5. Some Features of Glacial Surface Geology (after Tanfil'ev and Karpinski).



MAP 6. The Soil Zones and Districts (after Prasolov).



MAP 7. The Zones of Vegetation (Roman numerals) and more important Districts (Arabic numerals). After Busch, Fomin, Ilinski (from information of the Geobotanical Division of the Chief Botanical Garden in Leningrad), Novopokrovski, Tanfil'ev, the author, and others.

The forest outposts push northwards along the river valleys. Tanfil'ev attributes this to the better drainage of the valley slopes so that ice is not formed so close to the soil surface. Also the valley slopes are better protected from wind and those which face south are more warmed by the sun. Kihlman long ago called attention to the rôle of wind in promoting evaporation from trees in winter and thus hindering their northward migration, and **Gordyágin** and **Ivanov** have now carried out direct experiments and shown how great an influence this winter evaporation, which continues with remarkable intensity under conditions of extreme frost, may have on the geographical range of various trees.

II. CONIFEROUS FOREST (Taiga).

In the very broad zone of Taiga or coniferous forest with podsolised soil the spruces are the most important and widely distributed trees. There are two forms—the western, European, *Picea excelsa* Link. and the eastern, Siberian, *P. obovata* Ledb. These two may occur together and form hybrids which connect the types, as has been observed by Kihlman in the Kola peninsula, and also relatively far to the east at Tyulina (Gov. Vyátka) and at Krylov (Gov. Perm). In the second place stands the pine—*Pinus silvestris*. The ecological characteristics of spruce and pine determine the distribution and character of the coniferous forest of the zone in question. Some of the leading distinctions are set forth below (Morózov).

SPRUCE (Shade-bearing)

Grows well under the shade of pine.
Demands relatively rich and moist, but not boggy, soil.
The leaves are very plastic, so that the species shows great tolerance in respect of light conditions.

PINE (Light-demanding)

Cannot exist or grows badly under the shade of spruce. A relatively poor soil suffices for it. Xerophilous.
The root system is very plastic, so that the species has great freedom in respect of soils.

Thus the spruce is most widely distributed on clay soils because it overshadows and eliminates the pine, while the latter grows mainly on sand and peat.

1. SPRUCE FOREST (Pl. II, Phot. 1).

The most important type of virgin spruce forest is the *Piceëtum hylocomiosum*, the soil of which is characterised by a thick unbroken moss covering, consisting mainly of the following species: *Hylocomium proliferum*, *H. triquetrum*, *Hypnum schreberi*, *H. crista-castrensis*, *Dicranum undulatum*. These mosses grow very well together and form a remarkably independent community, which may exist in association with various coniferous trees. Thus **Gordyágin** has described it in forest of spruce, *Pinus sibirica* and *Abies sibirica* near Samarovo on the Obi, and I myself in forest of *Larix sibirica* and *Pinus sibirica* on the Altai mountains. The same moss community is also characteristic of *Pinetum hylocomiosum* (see below). Besides the species cited, Poly-

tricha, especially *P. juniperinum*, sometimes takes a considerable place in this moss community.

In his general description of the spruce forest of the Tartar republic Gordyagin gives the following more important characteristics. Besides the spruce *Abies sibirica* may form a considerable constituent, but other trees are either absent or occur as isolated individuals only. In the undergrowth *Juniperus communis*, *Sorbus aucuparia*, *Rhamnus frangula* and often *Prunus padus*, are characteristic.

The following are typical species of the layer of perennial herbs:

<i>Oxalis acetosella</i>	<i>P. rotundifolia</i>	<i>Goodyera repens</i>
<i>Circaea alpina</i>	<i>P. media</i>	<i>Orchis maculata</i>
<i>Linnaea borealis</i>	<i>Moneses grandiflora</i>	<i>Lycopodium clavatum</i>
<i>Vaccinium myrtillus</i>	<i>Tridentalis europaea</i>	<i>L. annotinum</i>
<i>V. vitis-idaea</i>	<i>Luzula pilosa</i>	<i>Equisetum silvaticum</i>
<i>Pirola minor</i>	<i>Maianthemum bifolium</i>	<i>Dryopteris phegopteris</i>

Rarer species are:

<i>Monotropa hypopitys</i>	<i>Neottia nidus avis.</i>
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According to Gordyagin, only the tree and moss layers of these spruce forests are well developed, the shrub and herb layers being of subordinate importance. This forest is characterised by marked podsol formation and the soil is greatly impoverished in mineral salts. The root systems of the trees are superficial and mycorrhiza formation is frequent.

Widely distant from the Tartar region and near the southern limit of the spruce, in Gov. Bryansk (formerly Orël), **Sukachev** describes spruce forest, of the same type (*Piceëtum hylocomiosum*) with the same five species of moss, occupying depressions where the ground water is close to the surface, and there is here again marked podsol formation, and considerable development of pan. This forest consists mainly of spruce, but isolated individuals of pine also occur. The woody undergrowth is scanty and consists of

<i>Acer platanoides</i>	<i>Quercus pedunculata</i>	<i>Rubus idaeus</i>
<i>Corylus avellana</i>	* <i>Rhamnus frangula</i>	* <i>Sorbus aucuparia</i>

The herb and dwarf shrub layer ("field layer" of the Scandinavians) is not closed and consists of

<i>Dryopteris spinulosa</i>	<i>Melampyrum pratense</i>	<i>Solidago virgaurea</i>
<i>Convallaria majalis</i>	<i>Milium effusum</i>	* <i>Tridentalis europaea</i>
<i>Equisetum silvaticum</i>	* <i>Oxalis acetosella</i>	* <i>Vaccinium myrtillus</i>
<i>Fragaria vesca</i>	<i>Pirola chlorantha</i>	* <i>V. vitis-idaea</i>
* <i>Luzula pilosa</i>	<i>P. secunda</i>	<i>Viola mirabilis</i>
* <i>Maianthemum bifolium</i>	<i>Peridium aquilinum</i>	

* Designates species given by Gordyagin as characteristic of the northern spruce woods.

In the same region Sukachev distinguishes another type of spruce forest, the *Piceëtum fruticosum*, on moderately moist, fairly rich soil with subsoil of cretaceous marl or phosphorite sand. This forest is dominated by spruce but has a considerable admixture of deciduous broad-leaved trees, such as *Quercus pedunculata*, *Acer platanoides*, *Populus tremula*, *Betula verrucosa*, *Ulmus pedunculata* Foug. The thick woody undergrowth consists of shrubs such as



Phot. J. Samsonov

Phot. 1. Spruce Forest on island in the Valdai Lake.



Phot. D. Yanichenski

Phot. 2. Pinetum hylocomiosum, with *Picea excelsa* sens. lat.
Kasan.

KEILER—VEGETATION OF THE PLAINS OF EUROPEAN RUSSIA.

Corylus avellana, *Euonymus verrucosus* Scop., *Tilia cordata*; and other representatives of deciduous forest are not infrequent. The herb layer also is rich and various, containing many representatives of the deciduous forest flora. The moss layer and indeed the constituent mosses themselves are absent.

North-eastern forest. In this, besides spruce and pine, *Abies sibirica*, *Larix sibirica*, and still further east, near the Urals, *Pinus sibirica*, come in as constituents (see map 7, of the distribution of species of trees), but mostly only as subordinate members of the community. All three are associated with spruce, but *Larix sibirica* also with *Pinus silvestris*.

In the district of Veliki-Ustyúg (Gov. Vólogda) Bitrisch describes an interesting type of forest with the following characteristics:

Top storey, open canopy: *Larix sibirica* 35.5–39.1 m., 200–250 years old.

Second storey: *Pinus silvestris* 28.4–32 m., 130–140 years old.

Third storey: *Picea* 14.2–21.3 m., 120 years old.

In more open places there is uninterrupted growth of spruce 30–50 years old.

Fourth storey (dwarf shrubs and herbs):

<i>Vaccinium myrtillus</i>	<i>Asarum europaeum</i>	<i>Pirola secunda</i>
<i>V. vitis-idaea</i>	<i>Dryopteris polypodioides</i>	<i>Rubus saxatilis</i>
<i>Oxalis acetosella</i>	<i>D. phegopteris</i>	<i>Lycopodium clavatum</i>
<i>Linnaea borealis</i>	<i>Goodyera repens</i>	<i>L. complanatum</i>

Fifth storey (mosses):

<i>Hypnum schroberi</i>	<i>H. crista-castrensis</i>	<i>Hylocomium triquetrum</i>
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The soil is sandy above, fairly dark coloured, podsolised, passing below into clay. There are fine inclusions and grains of calcium carbonate. *Larix sibirica* is indeed associated, in north-eastern Russia, with calcium carbonate.

Forests near the western limit of the Russian Taiga zone. These show the influence of approach to the milder west-European oceanic climate by a stronger admixture of deciduous trees and the presence of species which are at home in this climate. This is very clearly shown in Poland by such species as *Abies alba*, *Larix decidua*, *Fagus sylvatica* and *Carpinus betulus*, and by the presence of such distinctively western types as *Hedera helix* and *Taxus baccata*.

2. PINE FOREST (Russian *Bor*, plur. *Borj*).

The pine is mainly a tree of sandy and partly of rocky soil. In middle Russia there are extensive tracts of sandy deposits which give favourable conditions for the development of pine forest. Gordyagin long ago established the following four types of pine forest for the Taiga region, somewhat condensing Sernander's classification: Pinetum hylocomiosum (Pl. II, Phot. 2), cladinosum, sphagnosum, and herbosum.

In the Tartar republic the first-named type has a continuous carpet of the same five species which characterise the Piceetum hylocomiosum. Since the pine allows more light to pass through its crowns than does the spruce the shrub and herb storeys are more developed. Besides the shrubs which char-

acterise the Piceetum hylocomiosum *Rosa cinnamomea* and *Cytisus ruthenicus* are especially characteristic of the corresponding Pinetum.

The herb and dwarf shrub storey shows the following species:

<i>Pirola secunda</i>	<i>Anemone patens</i>	<i>Veronica officinalis</i>
<i>P. chlorantha</i>	<i>Lycopodium clavatum</i>	<i>Calamagrostis silvatica</i>
<i>Chimaphila umbellata</i>	<i>Fragaria vesca</i>	<i>Melica nutans</i>
<i>Melampyrum pratense</i>	<i>Antennaria dioica</i>	<i>Pteridium aquilinum</i>
<i>Hieracium umbellatum</i>	<i>Polygonatum officinale</i>	<i>Calypso borealis</i>
<i>Solidago virgaurea</i>	<i>Convallaria majalis</i>	<i>Gymnadenia cucullata</i>

Pinetum cladinosum is characterised by a lichen covering of fruticose *Cladoniae*—*C. silvatica*, *rangiferina*, *alpestris*, *uncialis*. Of mosses *Polytrichum piliferum* and to some extent *P. juniperinum* are characteristic, but in these lichen woods mosses are of subordinate importance.

The herb and dwarf shrub layer is characterised by the presence of a considerable number of species of dry sand and even of the steppes:

<i>Antennaria dioica</i>	<i>Dianthus polymorphus</i>	<i>Jasione montana</i>
<i>Artemisia campestris</i>	<i>Filipendula hexapetala</i>	<i>Koeleria glauca</i>
<i>Astragalus arenarius</i>	<i>Genista tinctoria</i>	<i>Sedum maximum</i>
<i>Campanula rotundifolia</i>	<i>Gypsophila paniculata</i>	<i>Silene otites</i>
<i>Centaurea marschalliana</i>	<i>Hieracium echinoides</i>	<i>Veronica spicata</i>
<i>Dianthus arenarius</i>	<i>H. pilosella</i>	<i>Vincetoxicum officinale</i>

These two types of pine forest retain their essential characters over a very wide stretch of the coniferous forest zone, and also farther to the south-east. Thus in the district of Kuznét'sk I found one of the most southern outposts of Pinetum hylocomiosum constituted as follows:

Woody undergrowth:

<i>Betula verrucosa</i> sol.	<i>Tilia cordata</i> sol.	<i>Euonymus verrucosus</i> spars.
<i>Sorbus aucuparia</i> sol.	<i>Populus tremula</i> (one)	<i>Rosa cinnamomea</i> (one).
<i>Cytisus ruthenicus</i> sol.		

Herbs and dwarf shrubs:

<i>Vaccinium myrtillus</i> cop.	<i>Hieracium umbellatum</i> sol.
<i>V. vitis-idaea</i> cop.	<i>Hypochaeris maculata</i> sol.
<i>Calamagrostis silvatica</i> cop.-spars.	<i>Lilium martagon</i> sol.
<i>Convallaria majalis</i> cop.-spars.	<i>Polygonatum officinale</i> sol.
<i>Maianthemum bifolium</i> cop.-spars.	<i>Pulmonaria angustifolia</i> sol.
<i>Pirola secunda</i> cop.-spars.	<i>Sanguisorba officinalis</i> sol.
<i>Pteridium aquilinum</i> cop.-spars.	<i>Serratula tinctoria</i> sol.
<i>Rubus saxatilis</i> cop.-spars.	<i>Solidago virgaurea</i> sol.
<i>Brachypodium pinnatum</i> spars.	<i>Viola montana</i> sol.
<i>Melampyrum pratense</i> spars.-sol.	<i>Antennaria dioica</i> unico loco. greg.
<i>Chimaphila umbellata</i> sol. (greg.)	<i>Trientalis europaea</i> unico loco. greg.
<i>Pirola rotundifolia</i> sol. (greg.)	<i>Epilobium angustifolium</i> 2 spec.
<i>Adenophora liliifolia</i> sol.	<i>Carex ericetorum</i> 1 spec.
<i>Aegopodium podagraria</i> sol.	<i>Lychnis viscaria</i> 1 spec.
<i>Anemone patens</i> sol.	<i>Trifolium lupinaster</i> 1 spec.
<i>Betonica officinalis</i> sol.	<i>Linnaea borealis</i> (found by V. Smirnov
<i>Chrysanthemum corymbosum</i> sol.	in this district).
<i>Galium boreale</i> sol.	

The moss covering was uninterrupted and consisted of the same five species already given (p. 201).

Pinetum sphagnosum may originate from an invasion of the forest by Sphagnum bog, or inversely a desiccating Sphagnum bog may be invaded by pines. The pine forest developed on poor sandy soil is generally accompanied by Sphagnum bogs in depressions.

III. MOSS PEAT MOORS.

These are everywhere characteristic of the coniferous forest zone, and often occupy extensive areas, among which villages with their cultivated patches lie like islands. Pedologists divide the coniferous forest region into two sub-zones—the northern podsol-swamp subzone, where the peat moors are especially widespread, and the simple podsol subzone.

The two principal ways in which the moss-peat moors are produced are by the growing up of lakes and consequent peat formation, and by the invasion of forest and of felled and burned areas by swamp. The spruce and pine woods show many stages of this conversion into peat moor. **Dokturóvski** and his fellow-workers have described the extensive moors of Polés'e in White Russia which have a special character. A typical picture is presented by the region of the affluents of the Prípyat (Pripet), which have a very slight fall, flow between low banks, and, in spring and after heavy summer rains, overflow the areas between neighbouring streams, so that the water from one river often passes into another. Immense tracts are thus occupied by moors, many of which bear herbaceous vegetation, but in general they are occupied by Hypneta and Sphagneta, under the influence of the ground water (which is very poor in mineral salts) or of the overflowing river water.

IV. EDAPHIC AND PHYSIOGRAPHIC VARIATIONS OF VEGETATION IN THE TAIGA ZONE.

The account given below has been kindly drawn up by Ramenski, and is based on his own observations and on data from the literature. It refers to the so-called "Lake Region" of north-western Russia—a region of typical moraine relief.

1. *Terrestrial communities on well-drained slopes.*

A. *Relatively rich little podsolised loam soils* are mostly occupied by good spruce forest with a herbaceous ground covering of *Asarum europaeum*, *Orobis vernus*, *Stellaria holostea*, *Betonica officinalis*, etc.: the humus is mild and neutral and the rôle of mosses negligible. On heavy clays and soils containing carbonates (Russian *poddubitsy*) in the south-west of the region oak woods flourish with a richer ground flora, containing the same species.

On the heavier and richer soils (clays and alluvium laid down in water) where there is more moisture, as in depressions and on the edges of swamps, the aspen is mixed with the spruce or oak, and dominance in the herb storey passes

to *Aegopodium podagraria*. Where moisture increases still further, the alder (*Alnus glutinosa*) appears and *Ulmaria palustris*, *Crepis paludosa*, etc., replace *Aegopodium*, while the forest grasses of drier habitats (*Melica nutans*, *Poa nemoralis*) are replaced by *Milium effusum* and *Deschampsia caespitosa*. The rôle of mosses is slight and the soil is more or less dark from humus and as a result of reducing processes.

B. *Sufficiently drained and moderately rich podsolised clay soils* bear spruce woods of the first quality. They are distinguished from the preceding by the greater rôle of the birch, especially after felling, and a lesser development of underwood. In the herb storey *Oxalis acetosella* is dominant and there is a good deal of *Vaccinium myrtillus*, *Maianthemum bifolium* and *Pirola*. There are few mosses and in deeply shaded spots the herb layer itself is scanty. The humus is mild.

With rise of moisture, increase of soil acids, and accumulation of raw humus the type of spruce forest deteriorates. Underwood is absent; the ground layer consists of *Vaccinium myrtillus*, *V. vitis-idaea* and *Maianthemum bifolium*, while cushions of forest species of *Sphagnum* appear (*S. girgensohnii*, in depressions *S. squarrosum*, sometimes *S. wulfianum*).

C. *Sandy soils* are occupied by pine forest, in the best drained places by thin pine forest of poor quality with little underwood, and the soil is covered with a more or less uninterrupted lichen carpet (*Cladonia silvatica*, *C. rangiferina*, *C. alpestris*)¹ mixed with forest mosses such as *Dicranum undulatum* and *Hypnum schreberi*, and the "field" layer has *Calluna vulgaris*, *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi*. The dry ridges of old dunes are covered with a continuous carpet of *Cladonia* and a thin herbaceous covering of *Festuca ovina*, *Antennaria dioica* and *Anemone patens*. The *Calluna* is especially characteristic of horizontal surfaces and decreases towards the north, where more hygrophilous plants like *Pteridium aquilinum*, *Vaccinium vitis-idaea*, *Calamagrostis silvatica*, etc., are co-dominant with it.

Moist pine forest occurs on sandy podsolised soils, the trees being closer set, more slender, and of better growth. There is a certain admixture of spruce and the undergrowth is better developed. Three variations are to be noted. (a) On the richer (neutral) sandy soils there is a relatively rich herbaceous flora, with *Pteridium*, *Rubus saxatilis*, *Maianthemum*, *Calamagrostis silvatica*, etc., and the mosses mostly suppressed. (b) On acid soils, especially with temporarily excessive water, *Vaccinium myrtillus* takes the place of the species mentioned, and in drier spots *V. vitis-idaea*. Besides the pine-forest mosses (*Hypnum schreberi*, *Dicranum undulatum* and *Hylocomium proliferum*), *Polytrichum commune*, *Sphagnum girgensohnii*, *S. recurvum*, *S. acutifolium*, *S. russovii* and *S. compactum* appear. (c) Over considerable areas the pine-forest mosses become dominant, and higher vegetation disappears, probably

¹ The lichen carpet is very often, but apparently not always, developed on areas which have been burned over.

owing to increased humidity of the air due to the neighbourhood of swamps, etc., but in the absence of temporary inundations.

In dry areas the forest was probably not originally continuous, but was interrupted by open spots covered with herbs and mosses which now occupy cleared and burned areas and meadows outside the valleys.

2. *Swamp and semi-swamp communities.*

These occupy flat, badly drained watersheds, depressions and valleys, also the sites of springs on slopes.

The oak or spruce woods of the loamy soils pass over, with increase of water content due to the topography, into *Alneta* with more or less rich underwood and herbaceous ground cover. The soil is black mud or strongly decomposed mineralised peat. Those which are not inundated very deeply or for long periods are marked by the dominance of *Carex caespitosa* and the presence of plants of wet meadows. *Alneta* which are inundated for long periods and mainly occur in river valleys have a marked swamp flora of *Carex vesicaria*, *C. gracilis* and *C. pseudocyperus*. Where there is much ground water containing mineral salts, as in some depressions and round springs, a *Hypnomagnocaricetum* is developed, with *Carex diandra*, *C. rostrata*, *C. paradoxa*, *C. caespitosa*, *C. dioica*, *C. chordorrhiza*, *Eriophorum latifolium*, *E. angustifolium*, *Calamagrostis neglecta*, *Liparis loeselii*, *Orchis militaris*, *Epipactis palustris*, *Menyanthes trifoliata*, *Pedicularis palustris*, *Parnassia palustris*, etc., and not infrequently *Saxifraga hirculus*. The mosses are *Acrocladium cuspidatum*, *Drepanocladus vernicosus*, *D. aduncus*, *Camptothecium nitens*, *Meesia triquetra*, *Paludella squarrosa*, *Bryum ventricosum*, *Helodium blandovii*, etc. Of trees and shrubs, besides *Alnus glutinosa*, there are *Salix cinerea*, *S. livida*, *S. myrtilloides*, *Betula humilis*, *B. pubescens*, *Picea excelsa* and *Alnus incana*. But the trees, such as the alder and birch, grow well and form closed forest only on a thin peaty layer or on peat which is at times dry and whose upper layers are strongly decomposed.

Picea and *Alnus incana* bear witness to a better natural drainage. Where there is a thick layer of constantly wet peat which is saturated with acid water containing $\text{Fe}(\text{HCO}_3)_2$ mosses preponderate over the higher vegetation, such plants as *Carex diandra* and *Eriophorum angustifolium* becoming sparse. *Betula humilis* is characteristic.

With increasing moisture the *Piceetum myrtillosum* becomes more open, and underwood of *Rhamnus frangula* and *Salix cinerea* preponderates. The thin peaty soil becomes covered with a continuous carpet of *Sphagnum* and other mosses, shaded by a thicker herbaceous cover of *Carex lasiocarpa*, *Phragmites communis*, *Calamagrostis lanceolata*, *Comarum palustre*, *Lysimachia palustris*, *Naumburgia thyrsiflora*, *Calla palustris*, etc. The trunks of trees grown over with moss bear forest species such as *Vaccinium myrtillus*, *Dryopteris spinulosa*, etc.

With increasing moisture Pinetum passes gradually into Sphagnum moor. Finally a vegetation based on a dry and often thick layer of peat—"Sphagnetum nanopinosum"—is produced, fed by atmospheric water. This mainly occupies the higher lying areas and alternates with wide stretches of low-lying "Sphagnetum scheuchzeriosum."

V. FRINGING ("GALLERY") AND "ISLAND" PINE WOODS IN THE GRASS-STEPPE ZONE.

Pine forest pushes far to the south into the Grass-steppe zone with chernozëm soil, where it occurs in restricted habitats of special character as *sand forest* and *chalk forest*. The *sand pine forests* are situated partly on exposures of the older Tertiary and other sands, but especially on the fluvio-glacial sandy deposits of river terraces lying above the river-side alluvial meadows. These sand terraces, exposed to strong winds, had at first the character of dunes, but were finally occupied by pine forest. Magnificent examples of such sandy pine forest are to be found in the neighbourhood of the town of Vorónezh and on the river Bityug near the village of Khrenovóe. Certain parts of the Vorónezh woods are Pinetum cladinosum: all five species of moss characteristic of Pinetum hylocomiosum occur, but they form only small tufts here and there. The soil cover often consists simply of a litter of pine needles, twigs and cones, with a scanty herbaceous vegetation. On the margins, along tracks and in clearings characteristic sand steppe plants occur—among others *Stipa joannis* Czel. var. *sabulosa* Pacz. Swamps occur between the dunes, and are inhabited by species of *Sphagnum* and other northern peat moss forms.

The Vorónezh and Khrenovóe pine woods are very rich in northern forms, e.g.

PTERIDOPHYTES.

Botrychium lunaria
Dryopteris phegopteris
Equisetum silvaticum
Lycopodium annotinum
L. clavatum
L. complanatum
Pteridium aquilinum

GYMNOSPERMS.

Juniperus communis
Pinus silvestris

ANGIOSPERMS.

Calluna vulgaris
Carex cricetorum
Chimaphila umbellata
Gymnadenia cucullata
Maianthemum bifolium
Monotropa hypopitys
Pirola chlorantha
P. minor
P. rotundifolia
P. secunda

ANGIOSPERMS.

Potentilla erecta
Rubus saxatilis
Trientalis europaea
Vaccinium myrtillus
V. vitis-idaea
Veronica officinalis

MOSESSES.

Dicranum undulatum
Hylocomium proliferum
H. triquetrum
Hypnum crista-castrensis
H. schreberi
Polytrichum juniperinum
P. piliferum

LICHENS.

Cetraria crispa
Cladonia alpestris
C. crispa
C. rangiferina
C. silvatica

Northern species of peat bogs and lakes (from Ramenski).

TREES AND SHRUBS.

Betula pubescens
Salix lapponum

CYPERACEAE.

Carex chordorrhiza
C. lasiocarpa
C. limosa
Eriophorum gracile
E. vaginatum

OTHER ANGIOSPERMS.

Comarum palustre
Drosera anglica
D. rotundifolia
Liparis loeselii
Malaxis paludosa
Menyanthes trifoliata
Molinia caerulea
Nuphar pumilum

OTHER ANGIOSPERMS.

Oxycoccus palustris
Scheuchzeria palustris
Utricularia intermedia
U. minor

MOSSES.

Aulacomnium palustre
Camptothecium nitens
Meesia triquetra
Polytrichum commune
P. gracile
P. strictum
Sphagnum dusenii
S. girgensohnii
S. medium
S. recurvum
S. squarrosum
S. subbicolor
S. subsecundum

These pine woods with *Sphagnum* bogs at one time penetrated much further to the south, but they have been destroyed by man. Thus I found on a terrace above the meadows liable to floods on the banks of the Medvédtisa, near the village of Sheremét'evka, great areas now bare of trees and occupied by blowing sand, and little *Sphagnum* bogs in the depressions with a whole series of northern species. Considerably further south Sukachev found similar bogs under similar conditions on the river Archeda where it flows into the Don, and discovered in them pine pollen and wood, the pine being now absent from this region in the wild state. On the right bank of the Volga near the village of N. Bannovka, in the district of Kamýshin, I found in a deciduous wood ordinary associates of the pine, viz. *Pirola chlorantha* and *P. secunda*. The conditions (presence of stony soil, etc.) made the former presence of pine forest quite probable. Again Vilenski describes a deciduous wood east of the Volga, on the river Eruslán, with birch and aspen as the principal trees. This is the last forest island on the edge of the Caspian depression, and here also *Pirola chlorantha* occurs.

The *chalk pine forests* occur in an elevated region on the right bank of the Volga, and also in the Govs. Vorónezh, Kursk and Khárkov (Pl. VII, Phot. 11). Northern associates of the pine, e.g. *Pirola secunda*, exist also in them, and certain rare plants which Litvínov regards as relicts of the Ice Age (see Section XIV, p. 226).

VI. OAK FOREST

(*Dubrava*, plur. *Dubravy*, Pl. III).

According to Morózov the oak is in Russia a species characteristic of the neighbourhood of the steppes. The oak region is a field of battle between forest and steppe, where under natural conditions the forest will obtain the upper hand. In accordance with this view the whole oak region of European Russia may be divided into three zones:

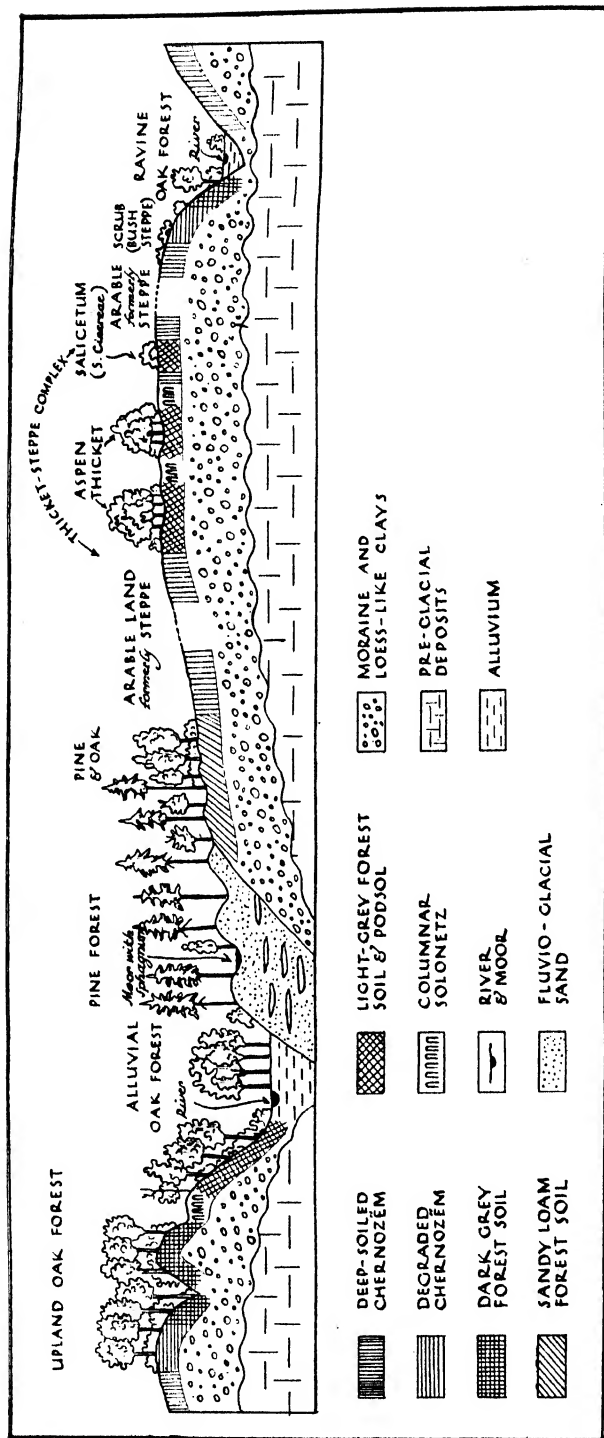


FIG. 1. Diagrammatic section across two river valleys with intervening plateau in the forest steppe region, showing the relation of topography and soil to the types of vegetation. For further explanation see text.

1. The belt of old forest steppe or of continuous oak forest where the struggle has been brought to a conclusion with the victory of the forest, and the loess (earlier steppe soil) is occupied by it. This forest zone is now split into fragments owing to the extensive destruction of the forest by man.

2. The belt of the existing forest steppe where the oak is developed in island-like clumps, near the banks of rivers.

3. The steppe belt, where forest is confined to ravines and does not extend to plateaux.

1. *Old forest steppe.* The "Túla-zaséki" and the forests on the Volga in Gov. Kazan are good examples. The former are part of the oak forests which at one time extended continuously through the Govs. of Kalúga, Túla, Tambóv and Kazan. It was called "Zaséki" because it protected the arable land of the Russian peasants against the incursions of the steppe nomads. Trees were felled and built into an impenetrable wall to stop the advance of these invaders. It is noteworthy that **Vysótski** discovered relics of steppe chernozëm in the podsolised forest soil of the Túla-zaséki, together with bones of steppe rodents (probably *Spalax microphthalmus* Güld.) filled with the dark chernozëm soil, and here and there unleached calcium carbonate.

The oak forest, like the spruce forest, occurs on clay soils, but the oak does not tolerate complete podsolisation and requires greater warmth than the spruce. It is true that the oak penetrates far to the north in the coniferous forest region, but there it reaches furthest in the river valleys where the soil is warmer and less podsolised, giving way to the spruce on the elevated clay soils (Morózov).

2. *Existing forest steppe.* In this zone the forests penetrate far to the south along the river valleys forming "gallery woods" along the high and steep river banks. The accompanying diagram (Fig. 1), from Tanfil'ev and Morózov is applicable to a very large part of the steppe region between the rivers Dnieper and Volga. It will be seen that the left bank of the river (left of the diagram) is higher and steeper. The subsoil is clayey (loess-like and moraine clay), but here and there (not shown in the diagram) are abundant chalk outcrops. The right bank of the river passes into a raised terrace of fluvio-glacial sand. This sand, which was exposed to wind action and assumed the character of dune, was later occupied by pine forest.

The oak forest occupies the higher and drier portions of the right bank with well grown trees, and also the steep left bank, passing some distance on to the plateau beyond. The characteristic changes of the soils are also shown in the figure. Above, on the plateau, which the oak forest did not reach so early, the chernozëm soil still exists, though it is degraded; passing thence into the river valley one meets first dark grey forest soil, and then light grey podsolised forest soil. In swampy places alder forest occurs. Further from the river, where sand begins to give place to clay, there is a peculiar mixed forest with an upper storey of pine and a lower storey of oak. Here and there, in the angle

enclosed by the confluence of two considerable rivers and where the courses of the two rivers approach one another, the oak forest occupies extensive areas of the plateau. Such are the upland oak forests, of which the famous Tellermann's and Shípov's woods (Gov. Vorónezh), used by Peter the Great for the building of ships for the Sea of Azov, are examples.

The communities of these upland oak forests have a complicated structure, in correspondence with the soil changes, as shown in Tables I and II.

Table I. *Number of stems (about 80 years old) per hectare in Shípov's wood, in relation to different soils (Stepánov).*

Soil type	Quercus pedunculata	Fraxinus excelsior	Tilia cordata	Acer platanoides	Ulmus spp.
Chernozëm	318	250	52	204	24
Forest clay soil	444	152	56	193	12
Solonéts-like soil	1023	90	nil	nil	nil
Solonéts	1440	nil	nil	nil	nil

Table II. *Composition of oak forest on various soils (district of Bobrov, Gov. of Vorónezh, after Gumann). Number of stems per hectare.*

Soil type	Layers of canopy	Quercus pedunculata	Fraxinus excelsior	Tilia cordata	Acer platanoides	Acer campestre	Acer tataricum	Ulmus glabra Huds. (U. scabra Mill.)	Ulmus nitens Moench (U. glabra Mill.)	Pirus communis	Total	Mean height in m.	Mean diameter in cm.	Mean age in years
Dark grey forest soil*	1	76	20	nil	nil	nil	nil	nil	nil	nil	96	29.5	77.9	160
	2	72	216	80	148	nil	nil	36	40	nil	592	16.3	15.6	60
	3	nil	nil	20	16	nil	nil	8	4	nil	48	8.5	—	30
Solonéts-like soil	1	162	504	522	66	nil	nil	20	46	nil	1320	11.2	13.7	60
	2	6	144	474	132	nil	nil	12	24	30	822	—	—	—
Solonéts		836	968	40	nil	56	48	nil	88	nil	2036	9.0	8.9	60

* Besides the three layers of tree canopy there are two lower storeys of vegetation: underwood and herb-layer.

We may conclude from these tables, that the forest developed on the most favourable soil has the most complex structure and the best grown trees, and that on the least favourable soil (solonéts) the trees are much more numerous in individuals and there is no one species dominant. The soil is occupied with difficulty and only as it is gradually changed. The trees are badly grown, much smaller in height and diameter, and the canopy is not differentiated into layers.

The following characteristics of these upland oak woods may be cited.

(1) Since the oak unfolds its leaves very late the lower storeys of the forest are well illuminated up to late in the spring, and consequently there is an abundant development of early flowering woodland herbs which give the forest the appearance of a flower garden (Pl. III, Phot. 4).



Phot. 3. Summer in the Oak Forest (Steppe zone). Gov. Vorónezh.



Phot. P. Nikitin

Phot. 4. Beginning of spring in the Oak Forest (Steppe zone). *Scilla sibirica* Andrz. with flower buds growing through the snow.

(2) In the summer there are few flowers and the herbaceous layer has the character of shade vegetation with leaf mosaics, etc.

(3) There is no continuous moss layer owing to the masses of fallen leaves and the relatively thick herb layer. Mosses are confined to the lower portions of the tree trunks and to steep bare places on the edges of ravines, etc.

(4) Myrmecochory is strongly developed among the herbs.

While the coniferous forests show a combination of tree growth with moss and lichen tundra, the deciduous forests show a similar combination with herbaceous communities. The steppe is dominated by herbs and though the herb communities of the forest differ both floristically and ecologically from those of the steppe the steppe vegetation is in evidence in forest clearings, along tracks and wherever the tree canopy is not too close.

3. *Ravine forest*. This is practically confined to the bottoms and sides of ravines which intersect the plateaux. Besides the plants of the upland oak forest of which a list is given on p. 214 the following occur, especially in the damp ravines:

Athyrium filix-foemina
Cystopteris fragilis
Dryopteris filix-mas
D. spinulosa

Actaea spicata
Geranium robertianum
Paris quadrifolia

Towards the south-east the oak penetrates a little even into the semi-desert zone, but here it is strictly confined to deep ravines with abundant freshwater springs, as on the Ergeni hills not far from Sarepta, which formed the old margin of the Caspian Sea. Here the oak is accompanied by very few representatives of the characteristic shade flora.

The oak in Russia is the representative of the central European deciduous forest, and correspondingly it grows best, according to Morózov, in the south-west and in Polés'e. In the east it suffers much from spring frosts. It has here a race which flowers and unfolds its leaves 2 to 3 weeks later in spring. Perhaps this can penetrate further east than the ordinary form. Near its northern and eastern limits the oak gradually loses its typical associates, so that the structure of the forest is modified. Thus in Gov. Vorónezh ash is freely mixed with oak, but further east the ash soon disappears.

According to topographic and edaphic conditions the oak forest may be divided into several types. Thus in each of the three regions, (a) west of the Dnieper, (b) central region, (c) east of the Volga, Vysótski divides it into the following types:

(1) The dry side towards the steppe.

(2) Massive central oak forest.

(3) The moist side (relict oak forest where it gives way to the spruce).

Further details cannot be given here.

List of oak forest species from observations in Gov. Vorónezh (Pl. III, Phot. 3 .

WOODY PLANTS.

<i>Acer campestre</i>	<i>E. verrucosus</i>	<i>Rhamnus catharticus</i>
<i>A. platanoides</i>	<i>Fraxinus excelsior</i>	<i>Tilia cordata</i>
<i>A. tataricum</i>	<i>Lonicera xylosteum</i>	<i>Ulmus nitens</i> Moench (U.
<i>Cornus sanguinea</i>	<i>Pirus communis</i>	glabra Mill.)
<i>Corylus avellana</i>	<i>P. malus</i>	<i>U. glabra</i> Huds. (<i>U. scabra</i>
<i>Crataegus monogyna</i>	<i>Quercus pedunculata</i>	Mill., <i>U. montana</i> Stokes)
<i>Euonymus europaeus</i>		

SPRING-FLOWERING EPHEMERALS.

<i>Adoxa moschatellina</i>	<i>Corydalis solida</i>	<i>Gagea lutea</i>
<i>Anemone ranunculoides</i>	<i>Dentaria quinquefolia</i>	<i>Lathraea squamaria</i>
<i>Corydalis marschalliana</i>	<i>Ficaria verna</i>	<i>Scilla sibirica</i>

GRASSES AND SEDGES.

<i>Agropyrum caninum</i>	<i>Carex michelii</i>	<i>Milium effusum</i>
<i>Brachypodium silvaticum</i>	<i>C. pediformis</i>	<i>Poa nemoralis</i>
<i>Bromus asper</i>	<i>C. pilosa</i>	
<i>Carex digitata</i>	<i>Melica nutans</i>	

OTHER HERBACEOUS PLANTS.

<i>Aegopodium podagraria</i>	<i>Neottia nidus-avis</i>	<i>Stachys silvatica</i>
<i>Asarum europaeum</i>	<i>Orobanch niger</i>	<i>Stellaria holostea</i>
<i>Asperula odorata</i>	<i>O. vernus</i>	<i>Viola hirta</i>
<i>Astragalus glycyphyllos</i>	<i>Polygonatum multiflorum</i>	<i>V. mirabilis</i>
<i>Campanula trachelium</i>	<i>Pulmonaria officinalis</i>	<i>V. odorata</i>
<i>Crepis sibirica</i>	<i>Scrophularia nodosa</i>	<i>V. silvatica</i>
<i>Galium cruciata</i>		

On the edge of the oak forest towards the steppe there is a fringe of trees and shrubs which tolerate dryness:

<i>Acer tataricum</i>	<i>Pirus communis</i>	<i>Rhamnus catharticus</i>
<i>Crataegus monogyna</i>	<i>P. malus</i>	<i>Ulmus nitens</i> Moench (U.
		glabra Mill.)

and of characteristic steppe shrubs:

<i>Amygdalus nana</i>	<i>Cytisus austriacus</i>	<i>Prunus fruticosa</i>
<i>Caragana frutex</i>	<i>C. ruthenicus</i>	<i>P. spinosa</i>
<i>Spiraea crenifolia</i>		

These trees and shrubs often also form independent communities of a peculiar dwarf wood or scrub, which is the first pioneer of woody vegetation on the steppe (and sometimes called "Bush steppe"). On the drier and more exposed places this scrub consists mainly of *Amygdalus nana* and *Caragana frutex*, and transitions may be observed to the taller scrub of *Prunus spinosa* and *P. fruticosa* and to the edge of the steppe woodland. The larger shrubs form veritable "gardens," many hectares in extent, and are exploited by the inhabitants in Govs. Tambov and Saratov. Associated with them are tall herbs, grasses and dicotyledons, the latter decorating such places with numerous flowers. Among these are:

<i>Agropyrum glaucum</i>	<i>Lavatera thuringiaca</i>	<i>Origanum vulgare</i>
<i>Bromus inermis</i>	<i>Libanotis montana</i>	<i>Veronica teucrium</i>
<i>Chrysanthemum corymbosum</i>	<i>Nepeta nuda</i>	

and many others.

On the Ergeni the oak is already rare, but in valleys and depressions of the slopes little woods still occur with *Ulmus nitens* Moench (*U. glabra* Mill.) predominant and many of the shrubs and tall herbs mentioned above. Where the depressions are shallow these little woods peter out, and often pass over into societies of *Spiraea hypericifolia*, which give way, where the depressions are shallower still, to the regular herbaceous vegetation of the steppe. On the east of the lower Volga the oak is rare in the last islands of woodland and is confined to strongly leached clay soils, but the communities of dwarf wood penetrate far into the semi-desert, and here *Spiraea hypericifolia* is characteristic and widely distributed.

VII. GRASS STEPPE—SEMI-DESERT—DESERT.

As one passes to the south, and especially to the south-east, the climate becomes drier and the summers hotter, and there is a gradual transition from grass steppe with its fertile "black earth" soil (chernozëm) to the desert of Turkestan with "grey earth" (serozëm) soil. The changes of the chief kinds of vegetation as we pass through the various soil-type zones are as follows.

The oak woods which are present on the northern chernozëm soils disappear on the leached chernozëm of the northern grass steppe region. Perennial and biennial dicotyledons, on the other hand, become abundant on the leached chernozëm, decrease on the deep-soiled and middle chernozëm types and rise again on the southern chernozëm, to reach a secondary maximum on the chestnut soils of the semi-desert. With drier conditions still they decrease on the burozëm (brown earth) soils and are absent in the true desert (serozëm) soil. Inversely the tussock steppe grasses, especially *Stipa* and *Festuca sulcata*, increase from the leached to the middle chernozëm and decrease again on the southern chernozëm and chestnut soils. Like the dicotyledons they do not reach beyond the burozëm soils. The xerophilous undershrubs with whitish felted leaves first appear on the southern chernozëm and increase steadily to the burozëm soils; they are still represented in the desert. The spring ephemerals exist in small numbers on all the chernozëm soils and rise proportionally through the semi-desert to the desert soils. Finally the lower cryptogamic plants of the soil surface are but slightly represented on the chernozëm soils, rise to a maximum on those of the semi-desert and fall again in the true desert.

In the course of this series the leaching of the soil in general diminishes from the more northern chernozëm to the serozëm. In the deep-soiled chernozëm 10 per cent. HCl effervesces only at a considerable depth, e.g. of more than a metre, but in the serozëm as a rule on the surface. According to **Tumin** the central region of deep-soiled chernozëm presents the most favourable conditions for the accumulation of humus, because on the one hand the soil is not so strongly leached as to impoverish it seriously in valuable nutritive material and on the other hand the effect of drought is not too severe. But nowhere in

the series is there any accumulation at the surface of easily soluble sodium salts (NaCl and Na_2SO_4). In the light chestnut and brown earth soils it is true that there is considerable accumulation of sodium sulphate, but this only begins at a depth of about 1.5 m. The following table shows some of the characters of these soil types:

	Deep-soiled chernozëm (after Tumin)	Light chestnut soils and burozëm (after Dimo)	Serozëm or svetlozëm (after Dimo)
Humus in surface layer	Mean 10.4 % Range 9.1-12.0 %	Chestnut 3.0-3.6 % Burozëm 2.1 %	1.1 %
General depth of humus horizon	105-120 cm.	Single determinations 44, 42, 39 cm. Range 32-52 cm.	Humus colour scarcely noticeable even on the surface
Beginning of effervescence horizon	40-110 cm.	24-46 cm.	Surface
Total content of mineral salts soluble in water expressed as per cent. of dry soil	At 1-5 cm. 0.032 % At 120-140 cm. 0.037 %	At 0-5 cm. 0.024 % At 90-95 cm. 0.042 % At 175-185 cm. 0.087 %	At 0-10 cm. 0.047, 0.016 % At 100-110 cm. 0.035, 0.019 % At 150-160 cm. 0.035 %
Cl down to 1.5 m.	Traces	Maximum 0.004 %	Very little
SO_3 down to 1.5 m.	Less than 0.005 %	Maximum 0.035 %	Very little

VIII. MEADOW STEPPE IN THE SUBZONE OF DEEP-SOILED CHERNOZËM (Plate IV).

At the height of its development at the end of May and the beginning of June the closed vegetation has the appearance of a flowering meadow. For instance, in the district of Vorónezh on the 11th of June, 1915, such a steppe showed innumerable bluish-lilac flowers of *Campanula simplex*, white heads of *Trifolium montanum* and fragrant cream coloured inflorescences of *Filipendula hexapetala*, with many other bright conspicuous blossoms. *Bromus erectus* was present in great masses with many inflorescences. But the basis of the vegetation was made up of the sod-forming steppe grasses *Festuca sulcata* and *Koeleria gracilis*. *Stipa joannis*, *S. stenophylla* and *S. capillata* were also present, but they were more or less scattered and did not suppress other species. The steppes described by **Sprygin** in Gov. Pénza, also on deep-soiled chernozëm, have a similar character. Besides the dicotyledonous herbs mentioned above, *Galium verum* and *Hypochaeris maculata* may be added as well as other species which appear where the soil is moister, e.g. *Chrysanthemum leucanthemum*, *Polygonum bistorta* and *Sanguisorba officinalis* (Phot. 5). This type of steppe may be briefly characterised as follows.

1. The turf-forming grasses form the basis but do not suppress numerous dicotyledonous herbs, which mostly form basal rosettes, but also raise assimilating leaves relatively high above the soil surface. The dominance of the sod-forming grasses in the northern variants is, according to Tumin, to be related to the relatively low fertility of the soil, and both the sod-forming



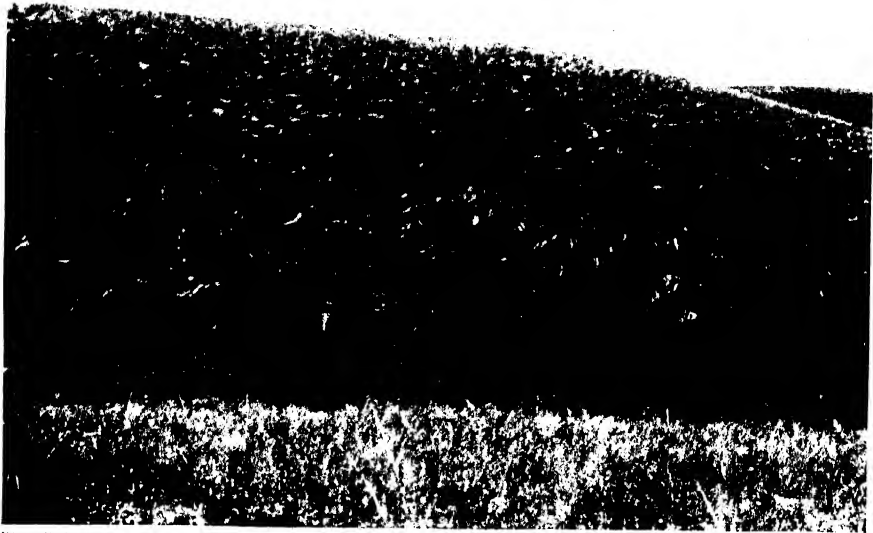
Phot. T. Popov

Phot. 5. Meadow steppe on the slope of a steppe valley in the neighbourhood of Oak Forest. *Stipa joannis*, *Dactylis glomerata*, *Filipendula hexapetala*, *Chrysanthemum leucanthemum*. Gov. Vorónezh, District of Usman.



Phot. B. Keller

Phot. 6. Meadow steppe (mowing meadow) with *Stipa joannis* dominant, forming part of a vegetation complex with Alder thicket. Steppe zone, Gov. Vorónezh.



Phot. T. Popov

Phot. 7. Tussock (*Stipa stenophylla*) steppe on the slope of a steppe valley.
Gov. Vorónezh, District of Novokhopersk.



Phot. B. Keller

Phot. 8. *Stipa lessingiana* steppe, Gov. Vorónezh, District of Valuyki.

KELLER—VEGETATION OF THE PLAINS OF EUROPEAN RUSSIA.

habit and the basal rosettes of the dicotyledons may also be correlated with the cutting of hay which is the rule in steppes of this type.

2. Spring ephemerals play but an insignificant part below the carpet of perennial herbs.

3. Lower plants, such as mosses, are conspicuous only in the northern variants of this vegetation.

The regular mowing of this type of steppe cannot fail to exercise an influence on the vegetation, but little has yet been done towards the solution of this problem. It is highly probable that species of *Stipa* and especially *S. stenophylla* were originally more widely distributed on these steppes, particularly on their southern portions, and that they approximated to the types of *Stipa* steppe. The cutting of hay would without doubt hinder the reproduction of this species from seed, since it ripens its fruits later than the ordinary time of hay harvest.

IX. STIPA TUSsock STEPPES (Plate V).

The deep-soiled chernozëm region and its vegetation passes over gradually towards the south and south-east into the ordinary or middle chernozëm region, and the meadow steppe also passes over into steppe characterised by the larger *Stipa* tussocks. It is not however by any means certain that this soil transition corresponds exactly with that of the vegetation. *S. stenophylla* and *S. capillata* are dominant on the *Stipa* tussock steppe, and the smaller turf-forming grasses such as *Festuca sulcata* and *Koeleria gracilis*, though widely distributed, play a subordinate part (Phot. 7). The *Stipa* roots branch profusely in the upper layer of soil and use most of the available water, thus restricting the dicotyledonous herbs, which, while common enough, are only scattered and do not form the gay flower garden of the meadow steppe. Such deep-rooting species as *Medicago falcata* however hold their own well with the *Stipas*, tapping a deeper layer of soil and remaining green and fresh late in the summer when the grasses are more or less burnt up (Gordyágin). The lower plants are not much in evidence (*Tortula ruralis* and *Nostoc commune* appear in consequence of cattle grazing) and the spring ephemerals, such as *Hyacinthus leucophaeus* and *Poa bulbosa* var. *vivipara*, have but a minor importance.

These *Stipa* steppes are ordinarily used for cattle grazing and it is not clear how far this use has an effect on their constitution. Nor is it clear from the literature whether *Stipa stenophylla* is most widely distributed on the ordinary or on the deep-soiled chernozëm.

Small tufted Stipa steppes. Here again the *Stipa* tussocks gradually lose their dominance, but not as in the meadow steppes owing to increase of moisture, rather indeed because of increased dryness. *Stipa tirsá* and *S. lessingiana* with small tussocks are the species here and *Festuca sulcata* again acquires more importance (Phot. 8). Dicotyledonous herbs have room for their root

development but their leaves are borne closer to the soil surface. So we gradually pass from the grass steppe to the semi-desert vegetation.

X. SEMI-DESERT VEGETATION (Plate VI).

This type of vegetation has the following characteristics.

1. The low growing sparse vegetation only covers one-third to one-half of the soil surface—bare soil is seen everywhere between the plants.

2. Steppe tussock grasses still occur but they are very scattered. The small tufted *Festuca sulcata* var. *vallesiaca* is dominant while *Stipa lessingiana* and *S. capillata* occur only as an insignificant admixture. Dwarf xerophytic under-shrubs with white hairy leaves play an important rôle, especially various forms of *Artemisia maritima* and also *Kochia prostrata* (Phot. 9). Among dicotyledonous herbs *Pyrethrum achillaeifolium* with leaves pressed close to the ground is important in the northern part of the semi-desert. Spring ephemerals and the lower plants have plenty of space for development and play a considerable part in the vegetation.

Further towards the desert the steppe grasses gradually disappear and the xerophytic under-shrubs acquire a correspondingly greater importance, and finally remain, with the ephemerals and the lower plants, as the typical desert vegetation (Phot. 10).

The above descriptions relate to uniform clayey soils and to those places where there is neither strong run off nor abundant accumulation of precipitation. There are many considerable variations due to local climate and topography, for instance the steppes in the neighbourhood of the Black Sea are very different in character from those of Samára.

The semi-desert and desert vegetation is especially under the influence of physico-chemical factors to which it reacts sharply. The deserts of Turkestan and the neighbouring mountains are, as has been said, a manufactory of species and types of xeromorphy and halomorphy. This region is a world of strong individualism in which plant communities are often difficult to recognise.

XI. LISTS OF FLORA OF STEPPE, SEMI-DESERT AND DESERT.

Flora of steppe on deep-soiled chernozëm. District and Gov. Vorónezh.

Two sample areas, each of 100 square metres. June 10–13th, 1926.

GRASSES AND SEDGES.

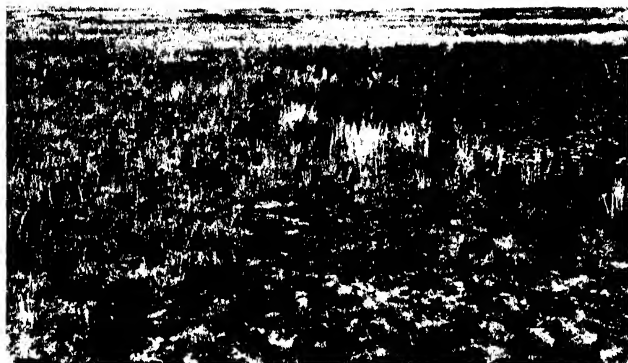
	Area 1	Area 2		Area 1	Area 2
<i>Festuca sulcata</i>	cop.	cop.	<i>Avena schelliana</i>	sp.-sol.	sp.-sol.
<i>Koeleria gracilis</i>	cop. 2	cop. 2	<i>A. pubescens</i>	sol.	sol.
<i>Stipa stenophylla</i>	sp.	sol.	<i>Hierochloë odorata</i>	cum.	—
<i>S. joannis</i>	sol.	sp.	<i>Bromus inermis</i>	—	sp.
<i>Bromus erectus</i>	cop.	cop.	<i>Agropyrum glaucum</i>	—	sol.
<i>Poa pratensis</i> var. <i>angustifolia</i>	cop.	cop.	<i>Carex praecox</i>	cop. 2	sp.
<i>Phleum boehmeri</i>	cop. 3	cop. 3	<i>C. supina</i>	sp.	sp.
<i>Agrostis canina</i>	sp.	sp.	<i>C. caryophylla</i>	sp.-sol.	sp.-sol.



Phot. B. Keller

Phot. 9. Semi-desert community—*Festuca sulcata* Hack. var. *calesiacae* and *Artemisia maritima* var. *incana* (*erecta* and *nuttans*). Near Sarepta.

Semi-desert community.
Festuca sulcata var. *calesiacae* *Artemisia maritima*,
var. *incana*. Compare
Phot. 9.



Grass steppe in desolation

Desert community,
Leontodon procumbens L.
Phoradendron monspeliense
on crustose-colum
saline soil.

Phot. B. Keller

Phot. 10. Grass steppe, semi-desert and desert communities in contact forming a complex on the Ergeni Hills near Sarepta.

STEPPE SHRUBS.

<i>Cytisus ruthenicus</i>	sol.	sp.-sol.	<i>Genista tinctoria</i>	—	sol.
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HERBS (nearly all *Dicotyledons*).

	Area a	Area b		Area a	Area b
<i>Draba repens</i>	cop.	cop.	<i>Silene otites</i>	sol.	sol.
<i>Thymus marschallianus</i>	cop.	cop.	<i>Stachys recta</i>	sol.	sol.
<i>Filipendula hexapetala</i>	cop.	cop. 2	<i>Stellaria graminea</i>	sol.	sol.
<i>Taraxacum vulgare</i> Schk.	cop.	cop. 3	<i>Taraxacum serotinum</i>	sol.	sol.
<i>Potentilla opaciformis</i>	cop. 2	cop. 2	<i>Thalictrum simplex</i>	sol.	sol.
<i>Achillea setacea</i>	cop. 3	cop. 2	<i>Tragopogon brevirostris</i>	sol.	sol.
<i>Campanula simplex</i>	cop. 3	cop. 3	<i>Trifolium alpestre</i>	sol.	sol.
<i>Euphorbia gracilis</i>	cop. 3	cop. 3	<i>T. pratense</i>	sol.	sol.
<i>Plantago media</i> var.	cop. 3	cop. 3	<i>T. repens</i>	sol.	sol.
<i>d'Urvilleana</i>			<i>Trinia henningii</i>	sol.	sol.
<i>Trifolium montanum</i>	cop. 3	cop. 3	<i>Verbascum phoeniceum</i>	sol.	sol.
<i>Galium verum</i>	sp.	cop. 2	<i>Veronica spicata</i>	sol.	sol.
<i>Arenaria graminifolia</i>	cop. 2	sol.	<i>Anemone silvestris</i>	sol.	—
<i>Fragaria viridis</i>	cop. 3	sp.	<i>Scorzonera purpurea</i>	sol.	sol.
<i>Veronica prostrata</i>	cop. 3	sp.	<i>Senecio jacobaea</i>	un.	sol.
<i>V. austriaca</i>	sp.	sp.	<i>Artemisia latifolia</i>	sol.	—
<i>Adonis vologensis</i>	cop. 3	sol.	<i>Aster amellus</i>	sol.	—
<i>Knautia arvensis</i>	sp.-sol.	sp.	<i>Betonica officinalis</i>	sol.	—
<i>Polygala vulgaris</i>	sp.-sol.	sp.	<i>Carduus hamulosus</i>	sol.	—
<i>Salvia dumetorum</i>	sp.-sol.	sp.	<i>Centaurea scabiosa</i>	sol.	—
<i>Thalictrum minus</i> var.	sol.	sp.	<i>Hieracium cymosum</i>	sol.	—
<i>nanum</i>			<i>H. pilosella</i>	sol.	—
<i>Asperula tinctoria</i>	sp.	—	<i>Inula hirta</i>	sol.	—
<i>Rumex haplorrhizus</i>	sp.	—	<i>Linaria biebersteini</i>	sol.	—
<i>Euphorbia sareptana</i>	sp.-sol.	sol.	<i>Medicago lupulina</i>	sol.	—
<i>Ranunculus poly-</i>	sp.-sol.	sol.	<i>Myosotis silvatica</i>	sol.	—
<i>anthemos</i>			<i>Orob. canescens</i>	sol.	—
<i>Senecio campester</i>	sp.-sol.	sol.	<i>Scutellaria hastifolia</i>	sol.	—
<i>Viola ambigua</i>	sp.-sol.	sol.	<i>Thesium cbracteatum</i>	sol.	—
<i>Ajuga genevensis</i>	sol.-cum.	sp.-sol.	<i>Verbascum orientale</i>	sol.	—
<i>Salvia nutans</i>	sp.-sol.	—	<i>Veronica chamaedrys</i>	sol.	—
<i>Anemone patens</i>	sol.-greg.	sol.	<i>Viola pumila</i>	sol.	—
<i>Iris furcata</i>	sol.-greg.	sol.	<i>Astragalus danicus</i>	—	sol.
<i>Achillea nobilis</i>	sol.	sol.	<i>Campanula bononiensis</i>	—	sol.
<i>Campanula sibirica</i>	sol.	sol.	<i>Convolvulus arvensis</i>	—	sol.
<i>Euphorbia procera</i>	sol.	sol.	<i>Coronilla varia</i>	—	sol.
<i>Falcaria rivini</i>	sol.	sol.	<i>Lathyrus pratensis</i>	—	sol.
<i>Galium boreale</i>	sol.	sol.	<i>Onobrychis viciacifolia</i>	—	sol.
<i>Jurinea mollis</i>	sol.	sol.	<i>Orob. pannonicus</i>	—	sol.
<i>Medicago falcata</i>	sol.	sol.	<i>Seseli annuum</i>	—	sol.
<i>Nonnea pulla</i>	sol.	sol.	<i>Silene chlorantha</i>	—	sol.
<i>Pedicularis comosa</i>	sol.	sol.	<i>S. viscosa</i>	—	sol.
<i>Phlomis tuberosa</i>	sol.	sol.	<i>Valeriana dubia</i>	—	sol.
<i>Picris hieracioides</i>	sol.	sol.	<i>Crepis tectorum</i>	un.	un.
<i>Potentilla argentea</i>	sol.	sol.			

SPRING EPHEMERALS.

	Area a	Area b		Area a	Area b
<i>Androsace septentrio-</i>	sol.	sol.	<i>Poa bulbosa</i> var. <i>vivipara</i>	little	little
<i>nalis</i>			<i>Veronica verna</i> sens. lat.	little	—
<i>Hyacinthus leucophaeus</i>	cop. 3	—			

LATE SPECIES (after mowing).

	Area a	Area b		Area a	Area b
<i>Euphrasia tatarica</i>	sp.-sol.	sol.	<i>Odontites serotina</i>	sol.	sol.

LOWER CRYPTOGAMS.

	Area a	Area b		Area a	Area b
<i>Cladonia pyxidata</i>	+	+	<i>Thuidium abietinum</i>	+	+
<i>Nostoc commune</i>	+	+	<i>Tortula ruralis</i>	+	+

Besides the above the following were found in the same steppe outside the two areas:

<i>Adonis vernalis</i>	<i>Dianthus campestris</i>	<i>Oxytropis pilosa</i>
<i>Arenaria longifolia</i>	<i>Dracocephalum ruyschiana</i>	<i>Ranunculus illyricus</i>
<i>Artemisia armeniaca</i>	<i>Echium rubrum</i>	<i>Sedum maximum</i>
<i>A. pontica</i>	<i>Gentiana cruciata</i>	<i>Senecio macrophyllus</i>
<i>Asparagus officinalis</i>	<i>Geranium sanguineum</i>	<i>Serratula heterophylla</i>
<i>Aster villosus</i>	<i>Helichrysum arenarium</i>	<i>S. radiata</i>
<i>Calamagrostis epigeios</i>	<i>Hieracium virosum</i>	<i>Sisymbrium junceum</i>
<i>Chrysanthemum corymbosum</i>	<i>Hypericum elegans</i>	<i>Stipa capillata</i>
<i>C. leucanthemum</i>	<i>Hypochaeris maculata</i>	<i>Veronica incana</i>
<i>Clematis integrifolia</i>	<i>Lavatera thuringiaca</i>	<i>Vicia cracca</i>
<i>Delphinium rossicum</i>	<i>Linum nervosum</i>	etc.

Flora of Avena desertorum meadow steppe. District of Kuznétzsk, Gov. Saratov. 460 sq. met. August 7th, 1905.

GRASSES.

<i>Avena desertorum</i> cop.-soc.	<i>Phleum boeheri</i> cop. 2
<i>Festuca sulcata</i> cop. 2-3	<i>Avena schelliana</i> sp.
<i>Stipa dasyphylla</i> cop. 3	<i>Bromus erectus</i> sol.
<i>S. joannis</i> cop. 3	<i>Calamagrostis epigeios</i> sol.
<i>S. stenophylla</i> sp.	<i>Hierochloë odorata</i> sol.
<i>Koeleria gracilis</i> sp.	

STEPPE SHRUBS.

<i>Cytisus ruthenicus</i> sp.-sol.	<i>Genista tinctoria</i> one
<i>Amygdalus nana</i> greg. in one place	

HERBS (almost all Dicotyledons).

<i>Anemone patens</i> cop. 2	<i>Knautia arvensis</i> sol.
<i>Artemisia sericea</i> cop. 2	<i>Linum flavum</i> sol.
<i>Filipendula hexapetala</i> cop. 2	<i>Medicago falcata</i> sol.
<i>Trifolium montanum</i> cop. 2	<i>Pimpinella saxifraga</i> sol.
<i>Achillea setacea</i> cop. 2-3	<i>Salvia dumetorum</i> sol.
<i>Inula hirta</i> cop. 2-3	<i>Sedum maximum</i> sol.
<i>Veronica spicata</i> cop. 2-3	<i>Artemisia armeniaca</i> one
<i>Hieracium ochioides</i> cop. 3	<i>Silene chlorantha</i>
<i>Thymus marschallianus</i> cop. 3	<i>Trinia henningii</i>
<i>Trifolium alpestre</i> cop. 3	<i>Androsace septentrionalis</i>
<i>Galium verum</i> cop. 3-sp.	<i>Arenaria graminifolia</i>
<i>Iris furcata</i> cop. 3-sp.	<i>Asperula tinctoria</i>
<i>Artemisia campestris</i> sp.	<i>Aster linosyris</i>
<i>Potentilla cinerea</i> sp.	<i>Campanula sibirica</i>
<i>Scorzonera purpurea</i> sp.	<i>C. simplex</i>
<i>Jurinea cyanoides</i> sp.-sol.	<i>Euphorbia gracilis</i>
<i>Centaurea marschalliana</i> sol.-greg.	<i>Hypochoeris maculata</i>
<i>Adonis vernalis</i> sol.	<i>Fragaria viridis</i>
<i>Antennaria dioica</i> sol.	<i>Phlomis tuberosa</i>
<i>Aster amellus</i> sol.	<i>Plantago media</i> var. d'Urvilleana
<i>Centaurea scabiosa</i> sol.	<i>Potentilla opaciformis</i>
<i>Chrysanthemum corymbosum</i> sol.	<i>Polygala vulgaris</i>
<i>Dracocephalum ruyschiana</i> sol.	<i>Scorzonera hispanica</i>
<i>Echium rubrum</i> sol.	<i>Stachys recta</i>
<i>Falcaria rivini</i> sol.	<i>Veronica chamaedrys</i> ¹
<i>Geranium sanguineum</i> sol.	<i>Vicia cracca</i> ¹
<i>Hieracium umbellatum</i> sol.	<i>Vincetoxicum officinale</i>

Moss. *Thuidium abietinum*, fairly abundant

¹ With *Amygdalus nana*.

Flora of semi-desert at Krasnoarméysk (Sarepta).

STEPPE-GRASSES.

Festuca sulcata var. *valcsiaca* cop.
Stipa capillata sol.
S. lessingiana sol.
Koeleria gracilis sol.

Pyrethrum achilleifolium cop.

SEMI-DESERT DWARF UNDERSHRUBS.

Artemisia maritima var. *incana* B. Kell. cop.-sp.
Kochia prostrata sp.-sol.

SUMMER AND AUTUMN ANNUALS.

Bassia sedoides cop.-sp.
Ceratocarpus arenarius sp.
Polygonum bellardi sp.
Salsola tamariscina sol.

SPRING EPHEMERALS (on the whole abundant)

Alyssum desertorum
Carex stenophylla
Draba verna
Poa bulbosa var. *vivipara*
Ranunculus polyrrhizos
Tulipe biebersteiniana
Veronica verna sens. lat.

REMAINING FLOWERING PLANTS.

Artemisia austriaca sp.
Achillea leptophylla sol.
Agropyrum cristatum sol.
Aster villosus sol.
Erysimum versicolor sol.
Statice sareptana sol.

LOWER CRYPTOGAMS ON THE SOIL.

Nostoc commune abundant
Microcoleus vaginatus v. abundant
Seytonema ocellatum v. abundant

More or less abundant.

Acarospora schleicheri
Cetraria steppae (C. *aculeata*)
Cladonia foliacea
Diploschistes scruposus var. *terrestris* Pers.
Riccia intumescens
R. sorocarpa
Ceratodon purpureus
Pterygoneurum cavifolium
P. subsessile
Tortula ruralis

Flora of the desert. Turkestan "Hunger steppe," Sprygin and Popóv.

29th April, 1911.

SUMMER AND AUTUMN ANNUALS.

*Halocharis hispida*¹ sol.-sp.
Girgensohnia oppositifolia un.

Veronica biloba sol.
Ziziphora tenuior sol.
Leptaliun ficifolium un.

SPRING EPHEMERALS.

Carex stenophylla cop.-soc.
Poa bulbosa var. *vivipara* cop.-soc.
Ranunculus severtsovi cop.
Gagea reticulata sp.

LOWER CRYPTOGAMS.

Collema sp.
Psora decipiens sp.
Thalloedema coerulesco-nigricans sp.

¹ On non-salty soils, dries in spring without flowering.

XII. VEGETATION OF THE SOLONÉTS AND SOLONCHÁK SOILS.

In dry climates the paucity of precipitation decreases leaching and gives the conditions for the accumulation of easily soluble salts which are injurious to ordinary plants. Russian pedologists distinguish two main types of such soils—*solonéts* and *solonchák*.

Solonéts soils. At a depth of about 10–15 cm. below the light eluvial horizon there is an extremely close textured illuvial layer which in dry weather splits into vertical columns. In moist weather this layer easily becomes wet and relatively impenetrable to water. The surface eluvial horizon is sometimes thin, forming a mere crust above the columnar layer ("crustose columnar" *solonéts* in contrast with the "deep columnar" type). The depth at which the columnar layer is formed and the variants of its structure depend on the original conditions of soil formation.

The deposit of salts in these soils begins at a certain depth below the columnar layer, and in the "crustose-columnar" soils, other things equal, nearer the surface. It is noteworthy that these soils maintain their general plan of structure over the great geographical area of grass steppe and semi-desert. This constant type of structure is characterised by the presence of Na_2CO_3 and by the washing out of colloids from the surface layer and their accumulation in the columnar layer. In the light chestnut and "brown earth" soils, also, this soda type of soil formation is found, though in less marked form, a somewhat close grained and darker coloured layer, corresponding with the columnar layer, occurring at a certain depth. But in the desert zone there are no solonéts soils, and the solonchák soils reach their greatest development.

Life-forms and behaviour of species on crustose-columnar solonets of the semi-desert. Krasnoarméysk (Sarepta).

<i>Species arranged in life-form classes</i>	<i>Average frequency</i>	<i>Assimilating parts during the summer</i>	<i>Root behaviour in re- lation to saline soil</i>
DWARF UNDERSHRUB WITH EPHEMERAL LEAVES			
<i>Artemisia pauciflora</i>	cop.	Mostly abundant	{ Roots penetrate to the deeper lying saline layers of soil
DWARF UNDERSHRUBS			
<i>Camphorosma monspeliacum</i>	cop.-cop. 2	Maintained	
<i>Kochia prostrata</i>	sol.		
SUMMER AND AUTUMN ANNUALS			
<i>Bassia sedoides</i>	sp.	Maintained	Root-system more su- perficial but pene- trates to the saline layers
<i>Polygonum bellardi</i>	sol.		
<i>Salsola tamariscina</i>	sol.		
SPRING EPHEMERALS			
<i>Alyssum desertorum</i>	{ On the whole very abun- dant	Plants in the seed or bulb (resting) state during the summer	Roots adapted to the non-saline surface layers (except <i>Tu- lipa biflora</i>)
<i>Ceratocephalus orthoceras</i>			
<i>Colpodium humile</i>			
<i>Gagea bulbifera</i>			
<i>Lepidium perfoliatum</i>			
<i>L. ruderale</i>			
<i>Myosurus minimus</i>			
<i>Tulipa biflora</i>			
LOWER CRYPTOGAMS ON THE SOIL			
<i>Nostoc commune</i>	cop.	Assimilating parts main- tained but strongly desiccated and in the resting condition	Plants attached only to uppermost non- saline layers or lying quite free on the soil surface
<i>Microcoleus vaginatus</i>	v. ab.		
<i>Scytonema ocellatum</i>	ab.		
<i>Acarospora schleicheri</i>	{ On the whole frequent		
<i>Aspicilia fragilis</i>			
<i>A. fruticulosa</i>			
<i>Cetraria steppae</i> (C. aculeata)			
<i>Dermatocarpon pusillum</i>			
<i>Diploschistes seruposus</i> var. terrestris			
<i>Endocarpon pusillum</i>			
<i>Kelleria polyspora</i>			
<i>Parmelia ryssollea</i>			
<i>P. vagans</i>			
<i>Rinodina nimbose</i>			
<i>f. sareptana</i> M. Tom.			
<i>Riccia intumescens</i>			
var. <i>typica</i>			
var. <i>incana</i>			
<i>R. sorocarpa</i>			
<i>Grimmia pulvinata</i>			
<i>Pterygoneurum cavifolium</i>			
<i>P. subsessile</i>			
<i>Tortula ruralis</i>			

Dimo long ago established the remarkable geographical correspondence between salt accumulation and soil type in these steppe and desert soils. In the northern portion of the grass steppe chernozem zone Na_2CO_3 is the

principal salt: further south and south-east it is replaced by Na_2SO_4 , further still, in the semi-desert, NaCl plays the chief part, though Na_2SO_4 is still present in considerable quantity.

In spring and autumn, and after heavy summer showers, the columnar solonét soils are transformed into temporary swamps, but in hot summer weather they dry out, exposing the vegetation to drought and great accumulation of salts. This takes place only at a certain depth, the surface layer being exposed to leaching. The increased salt accumulations are marked by outposts of the southern vegetation types. Thus on the areas of columnar solonéts in the steppe zone there occur semi-desert communities of *Festuca sulcata* var. *valesiaca* together with much *Artemisia maritima* var. *stepposa* (B. Keller), sometimes *Kochia prostrata* and much *Nostoc commune*. In the semi-desert zone on the columnar solonéts soils (mainly of the "crustose" type) desert vegetation begins. The steppe grasses go out and dwarf shrubs such as *Artemisia pauciflora* and *Camphorosma monspeliacum* attain importance. On one and the same soil in the semi-desert zone there are great variations and different combinations of vegetation because the actual edaphic conditions vary according to the different soil horizons (Pl. VI, Phot. 10).

In the northern part of the chernozëm grass steppe I observed *Silene besseri* and *Plantago maritima* on a basis of *Festuca sulcata*, as the first sign of increased salt content on areas of columnar solonéts with a clearly developed, though thin, surface layer.

Solonchák soils. These form the second type of soils rich in salts. In very dry regions, where damp soils are exceptional, there are wet areas marked by development of solonchák soils. The water is rapidly evaporated and replaced by new water from below, and even if the latter is fresh, there is eventually an accumulation of easily soluble salts (mainly Na_2SO_4 and NaCl) in the surface layers. Typical solonchák soils are moist even in hot summer weather owing to the proximity of the ground water.

In the grass steppe chernozëm zone solonchák soils are not very common. They penetrate furthest north in the characteristic vegetation complexes with aspen thickets (see below, p. 227) on the flood plains of the steppe rivers: also in steppe ravines and on slopes where the ground water is near the surface. In the semi-desert zone they are much more widely and strongly developed. Here in the Caspian depression there are many salt lakes, whose shores are occupied by extensive and various types of solonchák soils, forming little "solonchák deserts" with communities of *Halocnemum strobilaceum*. The Kirgiz call such a desert a *Khak*.

The vegetation of the solonchák soils of the semi-desert zone is very various according to the conditions of moisture and salt accumulation. Thus there is solonchák halophytic vegetation and there are also solonchák meadows, etc.



Phot. T. Gordejev

Phot. 11. Salt desert. *Atriplex canum* C. A. Mey. on saline soil.
Khanskaya Stavka.



Phot. B. Keller

Phot. 12. "Salt marsh" on solonchak (wet saline soil) with *Halocnemum
strobilaceum*. Ergeni Hills behind, with tree and shrub communities in the
depressions. Near Sarepta.

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Gradual transitions from solonéts to solonchák soils occur, and below is given a series of plant communities characteristic of these transitions on loamy soil in the semi-desert zone, both moisture and salt content gradually increasing. The single communities sometimes extend for many kilometres and form striking features in the semi-desert landscape.

XIII. PLANT COMMUNITIES AND SOIL CONDITIONS OF THE SALTY SEMI-DESERTS (Plate VII and Plate VIII, Phot. 13).

PLANT COMMUNITIES (dominants).

SOIL CONDITIONS.

- | | |
|---|--|
| I. 1. <i>Kochia prostrata</i>
<i>Camphorosma monspeliacum</i> | Considerable NaCl and Na_2SO_4 , but only beginning at a certain depth, weaker in (1) than in (2) and (3). |
| 2. <i>Artemisia pauciflora</i>
<i>Camphorosma monspeliacum</i> | Strong drought during the hot summer. |
| 3. <i>Nanophytum erinaceum</i> | The soils usually (but not always) belong to the crustose-columnar type (solonéts). |
| II. 4. <i>Anabasis salsa</i>
5. <i>Atriplex canum</i> (Phot. 11) | Very high content of NaCl and Na_2SO_4 , much greater than in I. Increasing salt and moisture. |
| III. 6. <i>Obione verrucifera</i>
7. <i>Petrosimonia crassifolia</i> | Extremely high NaCl and Na_2SO_4 content. |
| 8. <i>Halochemum strobilaceum</i> (Phot. 12) | Soil very wet even in summer. |
| 9. <i>Salicornia herbacea</i> (Pl. VIII, Phot. 13) | Moisture and salt increasing from (6) to (9). |

The following list represents the flora which can be considered more or less halophytic in the subzone of the deep-soiled chernozëm. It is taken from the vegetation complexes with aspen thickets (see below, p. 227) on the plateaux of Gov. Vorónezh (solonéts and solonchák soils—including solonchák meadow).

<i>Allium paniculatum</i>	<i>Plantago maritima</i>
<i>Artemisia maritima</i> var. <i>stepposa</i>	<i>P. maxima</i>
<i>Aster tripolium</i>	<i>P. minuta</i>
<i>Atriplex litorale</i>	<i>Polygonum arenarium</i>
<i>Atropis convoluta</i>	<i>Scorzonera parviflora</i>
<i>Bassia sedoides</i>	<i>Senecio grandidentatus</i>
<i>Carex stenophylla</i>	<i>S. macrophyllus</i>
<i>Cirsium acaule</i> var. <i>esculentum</i>	<i>Silaus besseri</i>
<i>Helicochloa schoenoides</i>	<i>Statice gmelini</i>
<i>Iris halophila</i>	<i>Suaeda maritima</i>
<i>Juncus gerardi</i>	<i>Taraxacum bessarabicum</i>
<i>Lepturus pannonicus</i>	<i>Triglochin maritimum</i>
<i>Peucedanum latifolium</i>	

The next list gives the plants of the solonchák soils, including solonchák meadow, and swamps from the neighbourhood of Krasnoarméysk (Sarepta) on the margin of the semi-desert of the Caspian depression. Neither list lays claim to completeness.

<i>Aeluropus litoralis</i>	<i>Centaurea galactifolia</i>
<i>Agropyrum elongatum</i>	<i>Cirsium acaule</i> var. <i>esculentum</i>
<i>Artemisia maritima</i> var. <i>salina</i>	<i>C. clodes</i>
<i>Asparagus trichophyllus</i> var. <i>trachyphyllus</i>	<i>Crypsis aculeata</i>
<i>Aster tripolium</i>	<i>Erythraea meyeri</i>
<i>Atriplex hastatum</i>	<i>Festuca arundinacea</i>
<i>A. litorale</i>	<i>Frankenia hispida</i>
<i>Atropis convoluta</i>	<i>F. pulverulenta</i>
<i>Bassia hyssopifolia</i>	<i>Geranium collinum</i>
<i>Capsella elliptica</i>	<i>Glaux maritima</i>
<i>Carex diluta</i>	<i>Gypsophila trichotoma</i>

<i>Halocnemum strobilaceum</i>	<i>P. maritima</i>
<i>Heleochloa schoenoides</i>	<i>Polygonum arenarium</i>
<i>Juncus gerardi</i>	<i>Salicornia herbacea</i>
<i>Lathyrus incurvus</i>	<i>Salsola soda</i>
<i>Lepidium crassifolium</i>	<i>Saussurea crassifolia</i>
<i>Leuzea salina</i>	<i>Scirpus maritimus</i>
<i>Lotus tenuifolius</i>	<i>S. tabernaemontani</i>
<i>Melilotus dentata</i>	<i>Scorzonera parviflora</i>
<i>Mentha pulegium</i>	<i>Senecio grandidentatus</i>
<i>Nitraria schoberi</i>	<i>Silaus besseri</i>
<i>Obione pedunculata</i>	<i>Spergularia salina</i>
<i>O. verrucifera</i>	<i>Statice caspia</i>
<i>Odontites scrotina</i>	<i>S. suffruticosa</i>
<i>Ofaiston monandrum</i>	<i>S. tomentella</i>
<i>Ononis hircina</i> var. <i>spinescens</i>	<i>Suaeda maritima</i>
<i>Orobanche cumana</i> (on <i>Leuzea salina</i>)	<i>Tamarix laxa</i>
<i>Petrosimonia crassifolia</i>	<i>Taraxacum bessarabicum</i>
<i>Peucedanum latifolium</i>	<i>Triglochin maritimum</i>
<i>Plantago cornuti</i>	etc.

XIV. SEMI-DESERT COMPLEXES.

In regions where little moisture is available for vegetation marked effects are produced by relatively slight changes of water content following the micro-relief. There results a great *complexity* of vegetation long ago exhaustively described by Dima and by myself in the semi-desert. On open plains a few steps will take one to an essentially different type of vegetation. The following elements make up the variegated soil and vegetation fabric of a semi-desert complex (Pl. VI, Phot. 10).

1. Grass steppe depressions in which a good deal of snow collects in winter and of which the soil is therefore more thoroughly leached. The soil is dark coloured and rich in humus. The vegetation is closed and from the low-lying centre changes towards the periphery where it passes into 2. The basis is often formed of *Festuca sulcata*, with *Stipa capillata*, *S. tirsia*, *S. lessingiana*. In the lower lying centre there is often *Poa pratensis* var. *angustifolia*, in spring *Ficaria verna*, and the like. Sometimes these hollows are overgrown with *Glycyrrhiza glabra*.

2. Semi-desert vegetation with light chestnut or brown earth soil on positive relief.

2-3. Transitions between semi-desert and desert types.

3. Desert vegetation on crustose-columnar soil. These solonéts soils are generally found in very slight depressions where there is temporary accumulation of atmospheric water, but not enough for thorough leaching.

The distribution of the vegetation in such a complex is here in general outlines the same as that of the geographical zones. Such complexes are widely distributed and characteristic on the plateau of Ergeni, and also to a considerable extent in the adjacent Caspian depression. For the compositions of the vegetation see the lists on pp. 218-226.

Aspen thickets.

The phenomenon of vegetation complexes is undoubtedly widespread in the most various regions. Here may be cited a very well marked example from the deep-soiled chernozëm grass steppe zone.

In the neighbourhood of the southern limit of the ice sheet, owing to a wide and fairly deep depression of the land, a great ice-tongue stretched far to the south up to the site of Stalingrad (Tsarítsyn). It planed and covered the old relief with a great sheet of ground moraine and thus produced a very flat area only slightly cut up by steppe valleys and therefore badly drained. In this region the development of aspen thickets (Pl. IV, Phot. 6) and the complex of solonéts and solonchák soils associated with them are characteristic. The thickets are restricted to the highest and flattest parts of the watershed with varied complexes depending on the micro-relief. In the deeper, mostly rounded, hollows the small aspen thickets grow on strongly podsolised soil. Here there may even be swamps with *Phragmites communis*, etc. Very slight depressions are occupied by deep and crustose-columnar solonéts soils. Grass steppe areas, with more or less damp meadows, solonchák soils, etc. also take part in the complex.

Popov has explained the evolution of the soils and plant communities of these areas. The areas of solonéts soils which hold the water in their impermeable columnar layers, carry the seeds of their own destruction. The water gradually leaches the soil, leading to podsolisation. When this process reaches a certain stage, *Salix cinerea* comes in, and later on the aspen. The characteristic flora of the aspen thicket shows the type of origin as islands in the dry steppe, since the species are distributed by birds and wind. This is one of the best worked out examples of the gradual conquest of steppe by forest.

XV. FACTORS HINDERING THE SPREAD OF FOREST SOUTH-EASTWARD.

The main factors militating against the occupation of the extensive southern and south-eastern steppes by forest, according to the views of various Russian authors, are as follows:

1. Lack of moisture in conjunction with the fine grained steppe soil. The precipitation of the steppe climate is markedly lower than that of the forest climate, more of the water is lost to the soil through immediate evaporation as a result of the steppe winds, penetration to the deeper layers of the soil is hindered by the fine grained nature of the surface, and the water which does penetrate cannot be so completely utilised by the root systems.

2. The strong steppe winds also have of course a direct effect on transpiration. Wind is in general the greatest enemy of trees, and not only the dry south-east winds of summer (often accompanied by the so-called "dry fog," Russian *mgla*) but probably also the winter winds have a great effect in preventing the spread of trees over the steppes just as they do over the northern

tundra, since Gordyagin and Ivanov have shown that trees, even in the leafless state, may lose considerable quantities of water

3. The presence of large quantities of easily soluble salts harmful to certain of the forest vegetation. But a clear picture of these effects is only seen where the deciduous forest reaches the solonéts soils, and even here a doubt remains as to whether the peculiar physical character of the soil does not affect the trees unfavourably. On the edge of these soils the sufferings of the trees are clear enough. They are dwarfed, of irregular growth, and the top, or even the whole tree, may perish: lichens settle in great numbers on the bark. The forest passes over the solonéts soils and cannot colonise them, at any rate without centuries of preparation. Patches of solonéts, still surrounded by crippled trees, are yet to be found in the forest. But where forest borders on pure steppe (i.e. with chernozëm soil) such pathological phenomena are not to be found.

4. Competition with the steppe grasses is probably also a factor. If acorns or the fruits or seeds of other trees are strewed among the grasses of a typical *Stipa* steppe (which as described on p. 217 form massive tussocks and exploit very thoroughly the water of the surface layer of soil) the seedlings abort. But if the grasses were completely extirpated without altering the soil itself the development of tree seedlings would probably take place.

It can be seen that the distribution of forest in the drier part of the steppe zone is often localised in places which from various causes are physiologically moister. The ravine woods and "gallery" woods are cases in point. And the farther one goes to the south-east in the dry steppe zone and then into the semi-desert and desert the more clearly and closely forest is confined to damper and more leached soils. In the so-called "forest-steppe" zone, however (i.e. in the transition region between forest and steppe), the forest often occupies areas which are apparently identical in conditions of soil and land relief with other areas which are occupied by steppe vegetation. And clear evidence of the advance of forest on steppe is not lacking. Thus forest invades the plateaux from the river valleys and can to a certain extent prepare the conditions for its own successful advance. Thus the wind has less effect on a close-set phalanx of trees than on isolated individuals, snow collects along the forest edge, and on its melting the snow water moistens and leaches the soil, leading to podsol formation and less favourable conditions for the steppe grasses, which are also shaded by the advancing trees. In the northern parts of the forest-steppe zone this advance is very marked. Burial mounds, which were undoubtedly made in open steppe, are now covered with trees.

Nevertheless in this northern region steppe often appears to be protected from forest invasion, and this has been attributed to fire, which might originate from lightning. Also the inhabitants of these regions have been acquainted with the use of fire since palaeolithic times. Such fires due to human agency may have been partly accidental, but it is also possible that the steppe was deliberately burned in order to destroy the litter of dead leaves and stems

which hinder new growth of the steppe plants. Again in certain historical periods fire was used by the Moscow kingdom as a means of protection against invading Tartars. The grass was burned over immense stretches so that the Tartars should find no fodder for their horses. Thus for instance in 1571 Prince Vorotýn'ski and his associates, by order of the Tsar, decided to set fire to the steppes at the time of the first autumn frosts when the grass was dry and before the snow fell, in clear weather and when the wind was blowing from the border towns towards the steppe. The Cossack villagers were ordered to burn the steppe in this way from the sources of the Vorona as far as the Dniester and Desná.

We cannot however regard the problem of the causes of the hindrance of the advance of forest on steppe as definitely solved. Many possible factors have been indicated and indeed every conceivable explanation has been brought forward, just as in the case of the American prairies. The proper weight and relative importance of the single factors have not been settled. Especially, little attention has been devoted to the different species of trees in this connexion. The causes of the failure of the pine, for instance, to spread on to the steppe may be quite different from those hindering the advance of oak or aspen. Certainly trees exist or could be produced, well adapted to occupy steppe. Even in desert such trees as *Arthrophytum* are able to invade. But the steppes are geologically recent and the available trees are few and are adapted on the whole to a damp climate. The characters of the individual species available must always be taken into account.

XVI. RELICT SPECIES OF THE GLACIAL AND TERTIARY PERIODS.

In the wild forest region of the distant Altai an extraordinarily interesting vegetation was discovered and described by Kryl'ov—nothing less than a relict oasis of the Tertiary deciduous forest with *Tilia* and a whole series of herbs characteristic of the European deciduous forest. The following species are the most interesting:

<i>Actaea spicata</i>	<i>Bromus asper</i>	<i>Festuca gigantea</i>
<i>Asarum europaeum</i>	<i>Campanula trachelium</i>	<i>F. silvatica</i>
<i>Asperula odorata</i>	<i>Cardamine impatiens</i>	<i>Geranium robertianum</i>
<i>Aspidium aculeatum</i>	<i>Circaea lutetiana</i>	<i>Sanicula europaea</i>
<i>Brachypodium silvaticum</i>	<i>Epilobium montanum</i>	<i>Stachys silvatica</i>

Part of the broad-leaved forest appears also to have maintained itself in the Urals. Thus Korzhinski and Ilyin have recorded four of the above: *Bromus asper*, *Circaea lutetiana*, *Festuca silvatica* and *Sanicula europaea*. Ilyin also adds *Scutellaria altissima*.

On the right bank of the Volga, in the middle and to some extent on the lower part of its course, there is an elevated region free from glacial deposits, but if the remains of Tertiary broad-leaved forest are also preserved here is not clear. According to the researches on the pollen preserved in peat which have recently been made by Gerásimov the oak invaded the plains of eastern Europe from the west, the spruce from the east, after the melting of the ice.

But certain herbs, e.g. *Festuca silvatica*, and probably also *Tilia cordata*, appear to have survived the Ice Age in this ice-free part of the Volga region.

It has long been known (Zinger, Litvinov) that on the exposures of chalk and limestone in the southern plains, on the edge of and beyond the limits of the glacial deposits, a considerable number of rare, partly endemic, plants exist, including species (or their close allies) which occur also on high mountains. Litvinov came to the conclusion that they have maintained their position since the glacial period, when the conditions of their existence closely resembled those now found on high mountains. Examples of these rare and partly endemic species are the following:

<i>Alsine setacea</i>	<i>Gypsophila litvinovi</i>	<i>Onosma simplicissimum</i>
<i>Androsace villosa</i>	<i>Hedysarum cretaceum</i>	<i>Pimpinella tragium</i>
<i>Anthemis trotzkiana</i>	<i>H. grandiflorum</i>	<i>Polygala sibirica</i>
<i>Artemisia hololeuca</i>	<i>H. polymorphum</i>	<i>Potentilla pimpinelloides</i>
<i>A. salsoloides</i>	<i>Helianthemum</i>	<i>Scabiosa isetensis</i>
<i>Astragalus albicaulis</i>	<i> chamaecistus</i>	<i>Schivereckia podolica</i>
<i>A. Zingeri</i>	<i>H. rupifragum</i>	<i>Serophularia cretacea</i>
<i>Bupleurum ranunculoides</i>	<i>Hyssopus cretaceus</i>	<i>Scutellaria alpina</i>
<i>Clausia aprica</i>	<i>Juniperus sabina</i>	<i>Silene cretacea</i>
<i>Daphne cneorum</i>	<i>Lepidium meyeri</i>	<i>S. supina</i>
<i>D. sophia</i>	<i>Linaria cretacea</i>	<i>Thymus cimicinus</i>
<i>Globularia vulgaris</i>	<i>Matthiola fragrans</i>	etc.

Litvinov also believes that *Pinus silvestris* on the chalk (Pl. VIII, Phot. 14) is a relict in the sense that it maintained itself here during the Ice Age beyond the limit of the ice. It is interesting that, of the rare plants in question, *Daphne sophia* actually occurs on the chalk in the pine woods which have maintained themselves or where they once existed.

A few notes on the distribution of these rare species may be added.

Daphne sophia Kal. occurs at a few places in Govs. Kharkov, Kursk and Vorónezh. This species is very near *D. altaica* Pall. which occurs in the steppe region on the south-western foothills of the Altai, on the rocks and stony slopes of the hills and lower mountains, and is also found on the Tarbagatai. An intermediate station of *D. sophia* exists in Gov. Orenburg in the southern Urals. One may add that another closely allied species of *Daphne*, *D. caucasica* Pall. occurs on the southern side of the Caucasus.

Besides the last small branches of the Urals in Gov. Samara and the elevated region on the Volga already mentioned, one may cite the parts of Govs. Vorónezh, Kursk and Kharkov which escaped the great glaciation as specially rich in species of this group. Especially interesting is Kozo-Polyanski's relict region in adjacent portions of Govs. Vorónezh and Kursk. Here such interesting species as *Bupleurum ranunculoides*, *Daphne cneorum* (described by Kozo-Polyanski as a separate species, *D. juliae*), *Gypsophila litvinovi* and *Schivereckia podolica* occur on the slopes of steppe ravines associated with a scrub of *Rhamnus catharticus*, *Cytisus ruthenicus*, *Amygdalus nana*, and *Prunus fruticosa*. The soil is dark coloured and thin, the chalk being almost



Phot. B. Keller

Phot. 13. Baskunkhak salt lake with *Salicornia herbacea* as pioneer on salt mud in the foreground. In the extreme distance is the great Bogdo mountain.



Phot. B. Keller

Phot. 14. Isolated pines on bare exposure of chalk representing the last remains of pine forest destroyed by human agency, Steppe zone. Gov. Vorónezh.

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or quite exposed in steep places. The vegetation is rich in characteristic steppe limestone plants and there are many elements which recall the Altaic steppes.

Bupleurum ranunculoides has three separate main areas of distribution, (a) the southern European mountains from the Pyrenees to the Balkans, (b) the Ural Mountains, (c) the mountains of central and northern Asia (the Altai and far to the east). If the label has not been changed the species was once found also in the Crimea. Finally it occurs (to our astonishment) on a small patch in Gov. Vorónezh. On the Altai this species occurs in the steppe meadows of the lower lying mountain region in company with many plants characteristic of the European steppes: also above the forest limit in mountain tundra and in subalpine meadows with characteristic subalpine species. Schröter draws an interesting picture of the "alpine steppe" in the Swiss Alps at 2120 m. near the forest limit. This is "dry meadow" with *Festuca sulcata* var. *vallesiaca* which in Russia inhabits the columnar solonéts soil, as one of the dominants: also *Koeleria gracilis*, *Phleum boeumeri*, *Poa bulbosa* var. *vivipara*, *P. pratensis* var. *angustifolia*, and *Bupleurum ranunculoides* associated, and characteristic alpine species as well.

This association of alpine and steppe plants is not a matter of chance. It cannot be doubted that the steppe vegetation has assimilated not a few mountain forms and the lichen and stony tundras of the high Altai have many points of resemblance to steppe, both in the general conformation of the vegetation and in the communities.

Grasses which are closely allied to steppe grasses play a leading part in these tundras as may be seen from the following three pairs of species.

ALTAI MOUNTAIN TUNDRA.
Festuca ovina sens. ampl.
Koeleria caucasica var. altaica
Avena versicolor

SOUTH RUSSIAN GRASS STEPPE.
Festuca sulcata
Koeleria gracilis
Avena schelliana

The characteristic steppe species *Avena schelliana* passes gradually over, in ascending to the higher mountain areas, into *A. versicolor*, the typical mountain tundra form. In the same tundra is a special, quite distinct species of *Stipa*—*S. mongolica*, and associated with it a widely distributed typical ice-age plant, *Dryas octopetala*.

A further series of characteristic steppe plants is represented by more or less closely allied forms in the alpine region of the Altai and these probably lived at one time close to the limits of the glaciers on the east European plains:

Achillea setacea
Campanula simplex

Galium verum
Myosotis silvatica

Senecio campester
Veronica spicata

Draba repens, again, which is found in the meadow steppe of Vorónezh, etc. also lives in Novaya Zemlya and occurs above the forest limit in the mountain pastures of the Altai.

Engler in his well-known work was not inclined to draw any sharp line between the glacial flora proper and the steppe plants which spread at the time of the development of glaciers. In fact part of the steppe flora is characterised more by its quick development and short vegetation period in relatively low temperatures than by its adaptation to hot summers and drought, and here perhaps a remote echo of Ice Age conditions finds expression. It is interesting also that there is no sharp separation between the animals of the Ice Age and the steppe species, as Obermeyer repeatedly says. We must then believe that a part of the flora which existed near the edges of the great ice sheet, and which contained many alpine elements, was assimilated to the steppe vegetation. Certain of these species maintained themselves on exposures of chalk, where the competitive struggle was not so severe, partly as a result of the constitution of the substratum itself. Part of this glacial flora which had collected in southern latitudes, advanced northward with the retreat of the ice sheet. The steppe elements of Sweden are perhaps the last remains of the vegetation in question, making their way there immediately on the heels of the ice sheet before the continuous forest belt had formed a broad barrier between the zone of the south Russian steppes and the north.

XVII. CHANGES OF VEGETATION UNDER THE INFLUENCE OF MAN.

Taliev has contributed much to the clearing up of these problems. Quite fresh traces of destruction and of the profound alteration of plant communities through human action are to be observed. The whole landscape may change as a result. In place of pine forest on sandy soil with its characteristic flora almost bare plains of drifting sand with very sparse vegetation consisting of steppe elements have been produced. Pine forest on the dark coloured chalk soil has been destroyed through the grazing of cattle and white chalk exposures with characteristic calcicole species have arisen (Pl. VIII, Phot. 14).

Taliev has expressed the opinion that the chernozëm grass steppe has been formed on the site of destroyed forest, but this view has not been generally accepted. Taliev does not believe with Litvinov that the rare and endemic chalk plants are relicts of the Ice Age. He points out that colonies of these species often appear on places which have had a great historical past and thinks that such species have occupied the sites of forest which has been destroyed. This author believes that the mass migrations of nomads along definite routes have greatly helped the distribution of plants, and it is possible that certain eastern species have actually migrated in this way. But great groups of facts (e.g. the distribution of *Bupleurum ranunculoides* referred to above) do not fit into this explanation.

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¹ Since it is impossible to give an even approximately complete list of the vast literature relating to the theme of my sketch of Russian vegetation, I cite only a few general works which mostly deal with extensive regions and contain many references, together with a few (marked *) written in German.

THE BEARING OF ECOLOGICAL STUDIES IN NEW ZEALAND ON BOTANICAL TAXONOMIC CONCEPTIONS AND PROCEDURE

By L. COCKAYNE AND H. H. ALLAN.

1. GENERAL.

ALTHOUGH this paper deals directly only with New Zealand we present it in the full belief that it has a fundamental bearing on taxonomy in general; for it cannot be that the lessons, both floristic and ecological, drawn from a region so self-contained and distinct as is New Zealand, can apply to that country alone. Further, in its intense endemism, its extreme isolation, its vegetation in part virgin, its varied climate, and its striking diversity of plant communities, New Zealand, as a field for fundamental taxonomic research, surpasses the highly cultivated lands of Europe whence taxonomic procedure was derived long ago.

The data and conclusions presented below are a result of a continuous study of the New Zealand vegetation and flora throughout the region—the Kermadec and Macquarie Islands excepted—first by the senior author for no less than 38 years, and by his colleague for the past 14 years. The conclusions, then, are not derived at all from hearsay evidence but from first-hand field investigations.

In an unsigned review (5, p. 379) of the seventh edition of Bentham's *Handbook of the British Flora* we read "Modern field-botany tends so much towards ecology, and systematists often feel that the determination of species by ecologists is none too critical, that the need of a handbook with complete keys and adapted for field work, but based on a conception of smaller, and often more actual species, is greater than ever." With the general statement we are heartily in sympathy, but the parenthesis calls for comment. Nothing has been brought home more clearly to the botanical ecologist in New Zealand than the inadequacy of the existing Floras to his needs—an inadequacy revealed not merely in the necessarily incomplete analyses of many polymorphic groups, but also in the inconsistency of the procedure adopted, and the absence of any clearly defined principles governing that procedure. Indeed, before the ecologist could advance the understanding of many of the problems confronting him he had, perforce, to become a systematist himself. It is certainly not too much to claim that such progress as has been made in systematic work in New Zealand of recent years has been very largely due to the results established by ecologists. This is illustrated in the recently published (10) second edition of Cheeseman's *Manual of the New Zealand Flora*. A com-

parison with the first edition shows that the changes made are due, in the main, to the acceptance of the results of the ecological work of the senior author of this paper in his floristic publications of recent years. Apart from this, however, the *Manual* still adopts methods and principles that we consider no longer acceptable in the light of the new knowledge gained by ecological research. The time appears to be ripe for an examination of the whole matter of taxonomic procedure, and a statement, illustrated by specific examples, of the principles governing what may be called the *Natural* or *Field Taxonomy*, as opposed to the *Artificial* or *Herbarium Taxonomy* of the past. Such a statement should provide a sure basis for attack on the multiplicity of taxonomic problems awaiting solution, and so pave the way for the production of Floras adequate to the requirements of serious workers in all branches of botany—that such work will need the earnest co-operation of many minds, and will require many years for its realisation, none appreciate more fully than we do ourselves. At the outset we desire to emphasise that we call attention to this need in no spirit of depreciation of the great systematists who have concerned themselves with New Zealand Floristic Botany in the past. No one could more admire than we the foundational work accomplished, e.g., by Hooker, Kirk and Cheeseman, or more fully recognise our indebtedness to it. Without doubt the accumulated results of their devoted labours represent all that could possibly be done by the herbarium method. But to recognise our indebtedness is not to deny that future work must proceed on those other lines that lead to a much more exact knowledge of the facts as they present themselves in the field and in the experimental garden. That this advance is possible follows from the far greater opportunities offered by ecological studies of coming to grips with the problem of the status of the individuals met with in nature, as contrasted with the mere guesses through the examination of isolated, greatly insufficient material—often fragmentary—in the herbaria of the usual type. Up to the present our herbaria, whether private or public, have in no case adequately represented the manifold forms to be found, nor have the specimens been supported by anything more than scrappily and casually prepared notes. Indeed in most cases the specimen sheets bear but the name of the locality, the date of collecting, the collector's name, and perhaps the estimated attitude. On such inadequate material species after species has been founded, their authors never having seen the plants in their natural habitats.

2. SOME RECENT CONTRIBUTIONS TO THE SPECIES QUESTION.

Before entering into details as to our observations and views, it may be as well to briefly review some recent expressions of opinion upon the species question and its relation to other branches of botanical enquiry. It will hardly be necessary fully to traverse the ground already covered by the senior author (17, 21, 22, p. 161), but reference will be made to the salient features in the body of the paper. Clements (13, p. 56) has said, "Finally, while the ecologist

is willing to go even further than the systematist in recognizing minor differences, providing these are based upon statistical field studies and experiment and not upon herbarium specimens, the practical scientist is concerned primarily with real species rather than the many varieties and forms into which some of them fall." But what are the "real" species? While we recognise the value, from some points of view, of the so-called "Linnean Species," and "aggregate species," the connotation of these concepts has already become vague and indefinite, and we would rather insist that the "scientist" (i.e. the taxonomist) is concerned primarily with the individuals that he is studying and their particular status. As soon as we pass from the "individual" to the "species" we have passed from the region of fact to that of interpretation. And while statistical study may do much it cannot of itself solve the fundamental problem. That the taxonomist must base his conclusions on the study of the living plant as presented by nature in the field is the essence of our plea. His taxonomic descriptions should, as far as possible, be drawn up in the field also. As Diels (35, p. 71) puts it, "Weitaus am günstigsten ist es, die Beschreibung einer Pflanze nach urwüchsigen lebenden Material am Standorte entwerfen zu können."

Du Rietz (37, p. 236) says, "Die Grundeinheit der Systematik ist nämlich schlechtweg die Art, ganz unabhängig von ihrem grösseren oder kleineren Umfang in dem einem oder anderem Falle. Und das Kriterium einer Art ist immer dasselbe, nämlich das dass sie gegen alle anderen Arten in der Natur natürlich abgegrenzt ist." This dictum does not, however, seem to lead us very far on the journey towards solving the age-long problem of what a species is and how to recognise it when it is before us. "Das Ziel," he goes on, "des Systematikers ist das, die Arten in der Natur so gut kennen zu lernen, dass er soweit als möglich von den Phenotypen abstrahieren und trotz diesem der Genotypen sehen kann." We fear the goal is far distant! But if for "Phenotypus" and "Genotypus" we substitute "Compound Species" and "Jordanon," as defined later, then that in part is indeed the goal the taxonomist should have before him, a goal to which New Zealand ecologists are already making fair progress.

Lotsy (46, p. 22), from the point of view of genetics, has incisively summed up his views in the statement, "*The Linnean species is no species*. Yet up to the present moment, one has continued to speak of it as such, and this has caused endless trouble. Most decidedly the time has come to break with this wrong designation." With this we are in perfect agreement from the ecological-taxonomic point of view, and we find, as will be seen later, Lotsy's analysis and the terms he proposes so apt, convenient and free from ambiguous accretions that we have adopted them in our efforts to bring order out of the present — shall we say — chaos in New Zealand floristic work. But while we appreciate the logic of Lotsy's rigid restriction of the term *species*—"to designate a group of individuals of identical constitution, unable to form more than one kind of

gametes; all monogametic individuals of identical constitution consequently belong to one species"—we do not think such restriction of a term so long and universally used will ever receive general acceptance. It will be far better to provide a new name for the Lotsyan species. Certainly, in the Lotsyan sense, there is no single species *known* in the New Zealand or any other flora! If the definitions we give later are borne in mind we do not think our use of the term "species" will cause any confusion.

Turesson (55, p. 172) also argues for the necessity "of an intensive study of the Linnean species and their habitat types or 'races.'" But he decries the "making" of elementary species on insufficient data. He adds (55, p. 173): "There is another point of divergence in the unit conception of genecology and systematism—viz. the tendency of the latter to split the species into smaller ones, thus creating a swarm of units which all rank as 'species.' From a genecological point of view this is to mistake the bricks of the building for the building itself. Only so long as these small 'species' (elementary species, microspecies, vicarial species, etc.) represent ecotypes—a point which has to be investigated in each particular case—and only so long as they are presented as constituent parts of the community of individuals which we have called an ecospecies, do they tell us anything of the morphology of that community from a genecological point of view." Now, that forms have sometimes been called "elementary species" without adequate investigation can hardly be denied, and that an elementary species (or as we prefer, with Lotsy, to say, a jordanon) cannot be recognised from herbarium material alone we also emphasise. Thus Domin (36, p. 39) claims in reference to the species of *Koeleria*, "Meine Varietäten entsprechen wenigstens bei den polymorphen Arten etwa den Kleinarten im Sinne Jordans, Opiz' oder Kerners. Sie unterscheiden sich also meist durch Organisationsmerkmale und nicht bloss durch Anpassungsmerkmale. Bei den weniger variablen Arten habe ich oft auch solche Formen, die durch ein einziges wichtigeres Merkmal von dem Typus abweichen, als Varietäten bezeichnet (so z. B. *K. Niederleinii* var. *mutica*), wogegen sonst meine Varietäten meist durch mehrere Merkmale charakterisiert erscheinen." One is at once compelled to ask what is a sufficiently significant characteristic, and what are the criteria by which it may be recognised. Domin arranges the New Zealand forms of *Koeleria* into three species, one of which is divided into three varieties. But this treatment is based on herbarium material only, and that of a very scanty nature (judging from his citations he had seen at most only 8 specimens from 4 localities). While the investigations we have in progress show Domin's arrangement to be suggestive, it can by no means be considered a final and satisfactory analysis, and we are certain that herbarium material, even of a much fuller character, could not alone allow of an adequate treatment. As to the value of Turesson's conception of "ecotypes" and the extent to which his views are supported by New Zealand evidence we make some remarks in a later section. But we would again urge that it is the whole series of indi-

viduals that concerns the ecologist no less than the systematist. Metaphors are dangerous and should not be unduly pressed, but we would say that to understand the building one is forced to study not merely the bricks, but all of the materials of which it is composed, and find into what classes they fall.

The general nature of the problems to be discussed may be illustrated by the case of *Leptospermum scoparium*, certain forms of which are well known in the gardens of Great Britain. Though the "species" was named as early as 1776, and though plants referred to it are abundant and widespread, the group remains one of the most baffling in the flora, and to disentangle the complex presented by nature would be the work of many men for many years. In publishing their species the Forsters (38, p. 72) were content to say of it "fol. sparsis, ovato-lanceolatis." Hooker (42, p. 69) divided his herbarium material under the heads—"Var. α . Erect, leaves lanceolate. Var. β . *linifolium*. Erect, leaves narrow, linear-lanceolate. Var. γ . *myrtifolium*. Erect, leaves ovate, spreading or recurved. Var. δ . *prostratum*. Prostrate, branches ascending. Leaves ovate or orbicular, recurved." With further collecting it was found that there were numerous forms that could not satisfactorily be placed in any of Hooker's "varieties." Kirk (45, p. 157) accepted these varieties and added a new one—var. *parvum*—for a low-growing form with small flowers. Cheeseman (9, p. 160) accepted this treatment, but later (10, p. 589) followed Cockayne (21, p. 70) in rejecting them. [As Cockayne has said, "In no list of plants hitherto published, so far as I am aware, are these varietal names used, partly because New Zealand botanical authors have troubled little about varieties, and partly because the above do not represent true-breeding races. Kirk and Cheeseman both recognize these varieties of *Leptospermum*, but it is suggestive that the latter botanist assigns a habitat to var. *prostratum* only. This plant, however, there is every reason to believe, is merely prostrate owing to wind or some complex of ecological factors, and so has no right to a varietal name in the sense in which the term 'variety' is now generally used. I could easily send to Europe dried specimens of different forms of *L. scoparium*, taken from shrubs growing in close proximity, which would at once receive varietal and perhaps specific names from any taxonomist monographing the genus and unacquainted with the species as they grow. At the same time there are distinct and easily recognizable races of *L. scoparium* which come true from seed, but most of these as yet possess no distinguishing name."'] One such race was published on the strength of ecological investigation by Cockayne (20, p. 58) as var. *incanum*. In addition there occur forms with flowers of diverse hue from deep crimson, through shades of pink, to pure white, the deeply coloured forms being comparatively rare. There are also forms with "double" flowers, both pink and white, one of the latter having been described by Cockayne (22, p. 179) as *L. scoparium* Leonard Wilson. What occurs in nature, then, in this as in many other cases, is a series of forms producing a complex whole, with which the herbarium method has proved quite incapable of dealing.

Its manner of getting over the difficulty is to say "the species is highly variable"—a self-evident fact which can hardly explain itself! It remains therefore for the ecological method to be applied. From the complex have to be separated out the true-breeding races, the extent to which these hybridise and the nature of the progeny have to be ascertained, and in addition the effect of the environment has to be reckoned with. It is only by intelligent field observations supplemented by cultural experiments that such a task can be successfully concluded. Suggestions on these various lines of attack are made in the following sections. We refer in several places to Diels's important work (35), *Die Methoden der Phytographie und der Systematik der Pflanzen*, but the whole book deserves the full attention of taxonomists, treating, as it does, with a breadth of knowledge and vision, of all sides of the question. With Diels's conceptions we find ourselves in general in pretty close agreement.

3. POLYMORPHY.

Since a recognition of the diverse forms and causes of the polymorphy existing in nature lies at the root of our problem, some preliminary analysis of this question seems desirable. Owing to the misleading and loose use of the term "variability" we suggest it be replaced by the word "polymorphy." As de Vries (32, p. 32) puts it, "Nichts ist variabler als die Bedeutung des Wortes Variabilität. Manche Verfasser benutzen dieses Wort in einem so viel umfassenden Sinne, dass man gar nicht versteht, was sie meinen." By the term "polymorphy" we mean the fact that different members (e.g. leaves) of an individual organism may be of diverse forms, and that among individuals, presumably closely related, there may be similar divergence in the forms of the various members making up the organism. Polymorphy may be of the following different classes and grades; only a few examples of each are given:

(a) *Polymorphy in the Individual Plant.*

1. *Diversity due to stage of development of the members.* Leaves may differ according to age in their size, shape, tothing, degree of pubescence, etc. Stems may similarly differ in degree of pubescence, angularity of cross-section, etc. Flowers after fully opening may change in size of parts, lose parts, show colour changes, etc. Thus one form of *Aristotelia serrata* (Elaeocarpaceae) has flowers at first white then gradually deepening to a dark crimson. Fruits may change in size and colour, etc. Thus a form of *Coprosma propinqua* (Rubiaceae) may show fruits apparently ripe and of a light translucent blue, but when fully mature these may be almost black.

2. *Diversity due to stage of development of the whole plant.* Some 200 New Zealand species show more or less strongly marked dimorphy or even polymorphy as they progress from the juvenile to the adult stage. The change may be abrupt or gradual. Thus *Metrosideros robusta* (Myrtaceae) is first a small

epiphytic shrub and finally, as a huge tree, a forest dominant. It may, however, commence life on the ground, and then bloom as a shrub; plants so originating may be recognised by their being much-branched from the base, and not bearing a single trunk as in individuals beginning as epiphytes. *M. perforata* shows great diversity between the appressed climbing parts and the free-flowering parts. A number of trees commence life as densely divaricating small-leaved shrubs and end as canopy trees of ordinary form. A number of species may flower in the juvenile or semi-juvenile stage, and the inflorescences may show certain differences from those of the adults, e.g. *Pennantia corymbosa* (Icacinaceae).

3. *Diversity due to the appearance of reversion shoots on the adult plant.* In some cases a plant that has become completely adult later puts forth reversion-shoots of completely or partially juvenile form, e.g. *Elaeocarpus Hookerianus*. Adult *Pseudopanax crassifolium* var. *unifoliolatum* (Araliac) that has been defoliated by fire may become reclothed in foliage of semi-juvenile character.

4. *Diversity due to no definitely assignable cause.* In a number of species there is remarkable diversity among the fully developed leaves of the individual, e.g. in juvenile *Aristotelia fruticosa* (see 3, Fig. 1, p. 74).

5. *Diversity due to epharmonic response of various parts.* In one form of *Coprosma myrtillofolia* leaves in the interior of the plant may be strongly ciliated, while the majority of the leaves are smaller and perfectly glabrous; similarly shade-leaves of *Nothofagus cliffortioides* and *N. Solandri* are glabrous, while sun-leaves are densely tomentose beneath. Many plants show considerable changes in size between leaves in the shade and leaves exposed to sun and wind, e.g. *N. fusca*. In the form of *Aristotelia serrata* showing colour change of flowers from white to crimson, flowers in the shade may remain at a pink stage.

6. *Diversity due to segregation of parts in an individual hybrid.* A hybrid plant—*Nothofagus cliffortioides* \times *fusca*—is known bearing a large branch of purely juvenile *fusca* character. We have seen a herbarium specimen of *Olearia* (Compositae) bearing below thick, strongly toothed, waved, narrow leaves, and above thin, flat, untoothed or very obscurely toothed, broad leaves, suggesting the cross *Olearia furfuracea* \times *macrodonata*. We have a specimen of *Olearia* bearing leaves some of which have the pure white tomentum of *O. virgata*, others the rusty tomentum of *O. divaricata*, and others again of intermediate character. Messrs Thomson and Simpson have sent us a frond of a fern clearly *Asplenium flaccidum* \times *lucidum*, in which the lower pinnae are nearly *lucidum* in character, and the upper nearly *flaccidum*. Possibly much of the minor diversity shown in many individuals is due to partial segregation of characters in a hybrid plant, though distinct somatic segregation as in the examples cited may be a rather rare phenomenon.

7. *Diversity due to fungal or insect attack.* Examples of this type of diversity are usually fairly easily referable to their cause, e.g. the witches' brooms in

Nothofagus Menziesii, *Edwardsia microphylla* (Papilionaceae), *Discaria toumatou* (Rhamnaceae); the modified leaves on various galls, e.g. on *Shawia paniculata* (Compositae). Fronds of *Dryopteris glabella* attacked by a scale insect become markedly different from usual.

8. *Diversity due to seasonal differences in parts.* *Teuclidium parvifolium* (Verbenaceae) is described as having solitary flowers, but many individuals carry some few-flowered cymes, and according to our observations the relative proportion of these cymose inflorescences may differ on the same plant from season to season. There is no recorded case for New Zealand of change of sex in an individual.

9. *Diversity due to differentiation of sex.* In addition to the normally monoecious species there are others which occasionally show irregular differentiation of sex in the flowers on an individual plant. A plant of *Coprosma lucida* known to us bears both male, female and hermaphrodite flowers. Female *Rubus parvus* may bear some completely sterile flowers, owing to non-development of the gynoeceum.

10. *Diversity due to the combination of two or more of the above phenomena in the same individual.* It must not be assumed too hastily that some of the types of polymorphy just mentioned are too trivial to concern the taxonomist. Unless great care is taken in collecting specimens and in annotating them, mistakes of interpretation may easily arise. Specimens, notably of forest trees, are too often gathered without sufficient care being taken to see that the specimens are fully representative of the plant from which they were gathered. Thus *Panax longissimum* Hook. f. is based on juvenile *Pseudopanax crassifolium* var. *unifoliolatum*. The var. *luxurians* Cheesem. of *Teuclidium parvifolium* is based on a single, almost certainly epharmonic, form of *T. parvifolium*. Until his ecological researches had shown the true explanation the senior author had been inclined to consider certain small-leaved forms of *Nothofagus fusca* as constituting a distinct variety (see 54, p. 334). On the other hand, though juveniles of *Pittosporum tenuifolium* may have smaller leaves than adults, ecological observations have revealed that there also exists a small-leaved jordanon. Further examples of misinterpretation due to neglect of attention to these matters are mentioned later on.

(b) *Polymorphy in Groups of Related Individuals.*

1. *Diversity due to differences in the members of individuals, even in inter-jordanic offspring.* "No plant is exactly like any other." Even a "pure line" evidences these "fluctuations" about a mean.

2. *Diversity due to epharmonic response by individuals in different directions* A striking case is that of *Ranunculus Monroi*, described by the junior author (3, p. 75), where a number of other examples are given. Thus, too, the var. *minor* Cheesem. of *Lepidium tenuicaule* (Cruciferae) is an unfixed epharmonic form, due to habitat conditions. A plant of *Libertia ixioides* (Iridaceae) was

divided by the junior author into two clones, one planted in a fairly well-drained loam soil, and the other in a heavy, rather boggy, clay soil. In the first flowering season no differences could be observed, but in the second (a very wet one) the clone of the boggy soil had shorter leaves, less developed inflorescences, and far smaller flowers (± 1 cm. diam., as opposed to ± 2.3 cm. diam.). Inasmuch as size of flower and capsule has always been considered of specific importance in the New Zealand *Libertias* this observation is not without importance.

3. *Diversity due to the existence of closely related jordanons.* There are many examples of this diversity in the New Zealand flora, and further examples will be given later. Here may be instanced *Epilobium melanocaulon*, with its jordanic varieties *typicum* and *viride*. An important series of cases is where the jordanons show markedly different life-histories. Thus *Nothopanax simplex* in most parts of the main islands has a juvenile with leaves 3-5-foliolate, the leaflets long and narrow, deeply and irregularly lobed. The juvenile of the jordanon of the Subantarctic Islands has only ternate, toothed leaves. There is also a jordanon similar to this on the main islands.

4. *Diversity due to the existence of forms reproducing parthenogenetically.* There are no known examples of this in New Zealand, though probably investigation on proper lines would reveal their existence.

5. *Diversity due to hybridism.* This most prolific cause of diversity will be more fully dealt with in a later section. We may here cite the multitudinous forms arising from the cross *Hebe elliptica* \times *salicifolia*.

6. *Diversity due to more or less complete unisexuality of individuals.* An example is *Clematis indivisa* with its large-flowering male, and smaller-flowering female. The different species of *Pimelea* (Thymelaeaceae) may show hermaphrodite, dioecious or polygamo-dioecious flowers. The species of *Coprosma* are dioecious, but in some at least the flowers may bear the parts of the opposite sex in a more or less developed condition.

7. *Diversity due to combination of two or more of the above phenomena.* This is well seen in the case of *Hebe salicifolia*, to be dealt with later.

(c) *The Artificial Polymorphy of the Systematist—the Result of the Doctrine of “Variability.”*

Varying conceptions of the criteria of species, and failure to recognise the true status of individuals has often resulted in what may be termed artificial polymorphy. The process of “lumping” by those with conveniently elastic ideas of the limits of species has again and again resulted in the production of so-called “variable” species out of material that can really be separated into groups of comparatively uniform character. Lotsy (46, p. 41) has laid down the dictum, “The perplexity of the subject, to which Darwin refers, is caused, in my opinion, by the simple fact that inheritable variability does not exist.” Whether this “simple fact” is as certainly a fact as Lotsy would seem to

believe, no one at present can surely say, but it remains only too true that the hypothesis of a vague "variability" of species, to which no cause is assigned, and under which the most diverse forms are united as belonging to a single species, lies at the root of the inconsistent and confused treatment to be found in even present-day floras. With the recognition of the jordanon as the fundamental taxonomic unit a way out of the confusion is established. The conceptions of Hooker, based on his world-wide knowledge of forms, have so dominated New Zealand Floristic Botany that his views as to "variability" are here stated. In the justly famous *Introductory Essay to the Flora of New Zealand* (41, p. viii) he says in reference to the work of the systematist, "Except he act upon the idea that for practical purposes at any rate species are constant, he can never hope to give that precision to his characters of organs and functions which is necessary to render his descriptions useful to others, for in groups where the limits of species cannot be traced (or, what amounts to the same thing in the opinion of many, where they do not exist), the object of the systematist is the same as in groups where they are obvious—to throw their forms into a natural arrangement, and to indicate them by tangible characters, whose value is approximately relative to what prevails in genera where the limitation of species is more apparent." He goes on (p. x), "In tracing widely dispersed species, the permanence with which they retain their characters strikes the most ordinary observer," and, "out of more than twenty thousand species cultivated at one time or another in the Royal Gardens at Kew, how few there are which do not come up, not only true to their species, but even to the race or variety from which they spring." Further on (p. xiii) he remarks "the local botanist looks closer, perceives sooner, and often appreciates better, inconspicuous organs and characters, which are overlooked or too hastily dismissed by the botanist occupied with those higher branches of the science, which demand a wider range of observation and broader views of specialities." Then comes the classical instance of *Lomaria procera*, "The resident may find two varieties of this and many other plants, retaining their distinctive characters within his own range of observations (for that varieties often do so, and for a very uncertain period, both when wild and also in gardens, is notorious) and he may perhaps have to travel far beyond his own island to find the link I have found, in the chain of forms that unites the most dissimilar states of *Lomaria procera*." And (on p. xiv) we read, "the botanist who has the true interests of science at heart, not only feels that the thrusting of an uncalled-for synonym into the nomenclature of science is an exposure of his own ignorance and deserves censure, but that a wider range of knowledge and a greater depth of study are required to prove those dissimilar forms to be identical which any superficial observer can separate by words and a name." Considering these different statements together it appears that where Hooker was able to apply a natural method he recognised the existence of true-breeding races (jordanons), but where he was compelled to rely upon herbarium

material he became impressed with the number of intermediate forms that could be found, and since he was dealing with floristic botany on a very wide scale he was led to believe that "species vary in a state of nature more than is usually supposed." Unfortunately, as we think, it is the second view that has been mainly followed in New Zealand taxonomy far beyond the point where it had practical value. While sharing in Hooker's distaste for uncalled-for synonymy we consider it more correct at the present-day to say that "it requires a wider range of knowledge and a greater depth of study to arrive at the jordanons, the hybrids and the epharmones (as we define them in the next section)—all of which to herbarium taxonomy are entities of the same status, as being 'variants' of a type which itself may be equally one or other of these opposed groups—than to lump together into an unwieldy mass all forms that can be linked up into a series." The work of taxonomy, in a word, is neither to "lump" nor to "split" after superficial examination, but to analyse and to test, and this can only be done by ecological and genetic methods.

Another source of error not always duly guarded against arises from the changes that may occur to plants in the drying-press. The experienced botanist learns to allow for such changes, and to note them, but a systematist dealing with material prepared by some one else may unwittingly fall into misconceptions. For example, a form of *Notothlaspi australe* collected by the junior author on the Saint Arnaud range is possibly an undescribed jordanon, but has the pure white flowers characteristic of other forms. Specimens (at least those collected in wet weather) when drying changed in colour of flower to a distinct pink, and might easily be considered by a systematist unacquainted with the plant in the field as a distinct species.

(d) *Heteroblastic species.*

We have already mentioned the importance of adequate field knowledge of the life-history of these, but they have so much taxonomic importance that some further consideration is desirable. Incidentally we make brief mention of their important phylogenetic significance. Of special moment are those that flower in the juvenile or semi-juvenile ("Übergangs-Form") stage, or on reversion-shoots of juvenile or semi-juvenile character. Some examples are: *Podocarpus dacrydioides*, *Dacrydium intermedium*, *Paratrophis microphylla*, *Weinmannia sylvicola*, *W. racemosa*, *Edwardsia microphylla*, *Hoheria sexstylosa*, *H. angustifolia*, *Pseudopanax crassifolium* var. *unifoliolatum*, *Dracophyllum strictum*, *D. longifolium*, *D. arboreum*, *Parsonsia heterophylla*, *Pennantia corymbosa*.

Dacrydium intermedium as a juvenile has leaves up to 1.5 cm. long, rather laxly placed, linear, acute; by gradual stages the leaves pass into the form found on mature trees, scale-like, about 2 mm. long, ovate-triangular, obtuse, densely placed and appressed to the stems. The senior author (16, p. 17) has stated "Juvenile and adult shoots have no resemblance whatsoever. The

important point is, however, that in Stewart Island the actual adult stage is not everywhere met with, and juvenile trees of the open-leaved character bear cones abundantly. To this form Kirk gave the varietal name of *gracilis*." Kirk also (43, p. 224) remarks, "usually a smaller plant than the type, from which it differs in its slender branchlets and monoecious flowers." Goebel (40, p. 386) says "Ob diese blühenden Jugendformen durch äusseren Umstände vom Erreichen der Folgeform zurückgehalten werden oder 'Mutationen' ('sports') darstellen, kann nur durch Kulturversuche ermittelt werden." There seem other possibilities, but for this and similar cases Goebel's dictum as to the method of determination cannot be too strongly emphasised. Cheeseman (10, p. 117) using the herbarium method, for he had not visited Stewart Island, makes no reference to Kirk's variety. From our standpoint the variety cannot be upheld, but the possibility of an originally juvenile form becoming permanent cannot be ignored. The senior author's discussion (17, p. 25) of the case of *Edwardsia prostrata* and *E. microphylla* may be referred to. Diels (34, p. 108) after pointing out that flowering may ensue at different stages in the development and so produce forms of considerable morphological difference, remarks that mistakes may easily arise where the life-history is not fully known. He uses as one illustration the well-known case of *Campanula rotundifolia*—"Von ihrer blühenden Schattenform sagt Goebel mit Recht, sie würde 'in einem anderen Florengebiete und in grösserer Zahl gesammelt, wohl unbedenklich als eine von *Campanula rotundifolia* verschiedene Art betrachtet worden sein,'" and considers it certain that many other recognised "species" are in like case. He by no means rejects the possibility of originally epharmonic unfixed forms gaining finally "die Möglichkeit, durch Vererbung fest zu werden, und der anfänglich strikten Abhängigkeit von den exogenen Umständen sich mehr und mehr zu entledigen."

Earlier Diels (33, p. 296) had come to the conclusion that the extremely xerophytic character of certain New Zealand plants was not in accordance with their present environment, and to look upon them as "Abkömmlinge der Waldflora" (p. 246) which had become "fixed" in the course of time. The senior author (14, p. 279) from a study of seedlings tended to accept this idea and applied it to dimorphic species, citing with modified approval a statement in Strasburger's *A Text Book of Botany* (1898, p. 46), "A plant...repeats in its ontogeny its phylogenetic development." However, Diels's (34, p. 113) remarks on this head are certainly sound: "Das biogenetische Grundgesetz, das die infantile Form unter allen Umständen phyletisch tiefer stellen will, verstösst also in weiten Umfang gegen die Thatsachen. Es kann dazu verleiten, die Wahrheit in ihr Gegenteil zu verkehren. Umgekehrt schliesst es die Möglichkeit nicht aus, in einzelnen Fällen den phyletischen Sachverhalt richtig wiederzugeben." In view of the facts accumulating as to "somatic segregation" of hybrids of chimaeras of various types, the possibility must not be overlooked that in many of these dimorphic species an explanation

based on hybridism may be the correct one. Theories apart, it is clear that intensive study of the phenomena is a great desideratum, and that to be of taxonomic value specimens must be collected with the greatest care and fullness of data. Unfortunately it must be added that for New Zealand we have as yet no adequate details in regard, for example, to the comparative structure of the flowers on juveniles, semi-juveniles and adult parts.

Pennantia corymbosa occasionally flowers rather freely when still completely in the juvenile stage. The juvenile is a small-leaved closely divaricating shrub (there is a forest epharmane of much more open habit), passing into an adult canopy-tree with much larger leaves. Semi-adults may flower on both juvenile and adult portions, while flowers also may occur on reversion shoots of adult trees. So far as our observations go the inflorescences on juveniles are somewhat less developed and the individual flowers rather smaller than those on the adults. It would be easy to send to a herbarium systematist specimens so distinct that they would be regarded as belonging to different species (with "intermediates" or "hybrids") were the life-history unknown.

The importance of a thorough study of life-histories in the solution of taxonomic problems cannot be over-emphasised. Without such it is often quite impossible to arrive at the correct status of individual forms. Buchanan (8, p. 338), from dried material, listed *Hebe salicifolia* as occurring on Chatham Islands. This remained unquestioned till the senior author (15, p. 319) showed by ecological and experimental studies that the Chatham Islands' jordanon differed pronouncedly in life-history from any jordanon of *Hebe salicifolia* "in being always a low tree with a distinct trunk. Its seedling form is also quite distinct....The early leaves are very coarsely and deeply toothed....," and so for a number of characters. It was accordingly given the specific name *gigantea*. Although Cheeseman at first considered life-histories ineligible as marks of specific distinction, yet finally (10, p. 791) he accepted this disposition of the jordanon, and it is undoubtedly correct, yet mere herbarium specimens of adults could never have revealed the truth.

So, too, marked distinctions in the juvenile forms at once separate as distinct *Dracophyllum arboreum* from *D. scoparium*, *Edwardsia tetraptera* and *E. chathamica* from *E. microphylla*, *Pittosporum Turneri* from *P. patulum*, apart from any other characters. *Leucopogon fasciculatus* consists of at least two jordanons—one homoblastic the other heteroblastic, yet neither, so far, has received a varietal name. There are numerous cases that need further investigation. *Schefflera digitata* has two distinct juvenile forms—the one with leaflets serrate merely, as in the adults; the other with leaflets irregularly lobulate or pinnatifid. The senior author (17, p. 18) was inclined to treat these differences as epharmonic, but field evidence as to distribution suggests that it is rather a case similar to those just mentioned. This taxonomic differentiation remains, no matter what views be taken as to the phylogenetic questions raised. *Pseudopanax crassifolium* is usually divided into the varieties *uni-*

foliolatum and *trifoliolatum*. The former is certainly a most distinct compound, heteroblastic variety, but evidence that is accumulating as to hybridism between species of *Pseudopanax*, and between these and species of *Nothopanax*, results in *trifoliolatum* being badly suspect. Both field and experimental evidence are necessary for a solution of the problem. Of *Dicksonia lanata* Cheeseman (10, p. 22) remarks, "At Whangarei, Bay of Islands, and other northern localities this usually produces a short stout trunk, but to the south of Auckland it is invariably stemless. Possibly there may be two distinct varieties with a different geographical range, but so far I have failed to find distinctive characters to separate them." Further evidence is highly desirable, and should not be unduly difficult to obtain; but the possession of a trunk or its absence, if not epharmonic, should surely be an orthodox taxonomic character. The diverse degrees of development of a trunk in *Dryopteris pennigera*, however, is probably referable to diverse habitat conditions.

Whether a species be heteroblastic or not, its life-history needs close study. Kirk (45, p. 127) says of *Rubus parvus*, "This curious species may be an arrested state of *R. australis*." A study of the life-history of each lends not the slightest support to this suggestion. Cheeseman (10, p. 501) is undoubtedly correct, "A remarkably distinct species, always easily recognized by its small size, 1-foliolate leaves with sharply dentate margins, long-acuminate sepals, and large oblong fruit." There might be some colour for Kirk's suggestion, if applied to *R. Barkeri*, but that is certainly a hybrid between *R. parvus* and a form of *R. australis* or *R. schmidelioides*. Hybridism introduces complications and possibility of misunderstanding in regard to dimorphic species and the status of individuals. The whipcord Hebes are heteroblastic in development and also hybridise freely with several of the small-leaved Hebes of the *buxifolia-laevis* description. Some of the hybrids produced might easily be mistaken for prolonged juvenile forms. Indeed \times *Hebe cassinioides* was thus mistaken by the senior author (18, p. 219). But Petrie (51, p. 52) in rejecting this opinion, fell into the equal error of considering that the plants in question constituted a distinct jordanon, to which he accorded specific rank, and yet his species was made up out of a garden hybrid of unknown origin and a wild hybrid of probably another origin!

4. TERMINOLOGY.

Although we hope our practice will become increasingly clear as the detailed examples given are studied it is desirable to make a preliminary statement as to our usage of terms. Since it is the generally recognised business of a flora to attempt to provide means of identifying the individual plants met with, the individual necessarily becomes the starting-point, and very little study is required to realise that individuals fall into various categories. Linnaeus, as Lotsy (47, p. 2) points out, clearly recognised that "there was a fundamental difference between non-transmissible and transmissible diversity

within his species." "Varietates attente inspiciantur," but "Varietates levissimas non curat botanicus." Unfortunately the clear-cut division was forgotten, and Linnaeus's second dictum tended to be applied to all "minor" forms, and even in present-day floras references to "mere" or "trivial" varieties may be met with. Geneticists have brought botany back to the standpoint that of no form can it be properly said "non curat botanicus"; but taxonomists, perhaps naturally, in view of the difficulty of the task, and the inertia caused by the long-accepted taxonomic procedure, have lagged behind.

In certain groups of individuals such diversity as exists is of very small amount, and one individual so closely resembles another that the student has no difficulty in identifying them as to all intents and purposes "alike." If such a group of individuals is found to breed true among themselves we have a "jordanon." Lotsy's definition (46, p. 27) is adequate: "A group of externally alike individuals which all propagate their kind faithfully, under conditions excluding contamination with individuals belonging to other groups, as far as these external characters are concerned, with the only exception of non-inheritable modifications of these characters caused by the influences of the surroundings in the widest sense to which these individuals or those comprising the progeny may be exposed." Briefly, then, a jordanon is a true-breeding group of similar individuals plainly distinct from any other such group. So far as we know all individuals of the Kauri are closely similar, breed true, and thus the species *Agathis australis* is composed of but one jordanon. Such species we term "simple species."

Diversity of a different grade occurs where there are two or more closely related jordanons forming a larger group, which is itself clearly marked off from any other group, but in which the jordanons are so closely allied that to treat them as separate species would too much obscure this closeness of relationship. Such a group of jordanons we call a "compound species," the jordanons of which we term "*varieties*." A simple instance is that of the turf-like *Coprosma Petriei*, with its varieties *vera*—a jordanon with translucent faintly blue-stained drupes—and *atropurpurea*, with port-wine coloured drupes. Apart from this clear-cut distinction the varieties are practically identical, but each breeds true when crossing is impossible. Each jordanon of a compound species, if sufficiently distinct for a diagnosis to be drawn up that will enable it to be recognised in the field, is given a varietal name, and if the varietal name is not cited the whole compound species is understood to be referred to. Where two jordanons can only be separated by genetic analysis and no diagnoses suitable for field work can be drawn up they may be included under a single varietal name, the variety thus being a compound one. According to our method the type, if founded on a jordanon, must receive a varietal name. Thus the whole content of *Coprosma Petriei*, as at present known, is referable to either var. *vera* or var. *atropurpurea*, not to a "type" with two "varieties" of it (Cheeseman's type is referable to var. *vera*). A simple species logically

should have a varietal name, but practically this seems unnecessary. Where there is danger of confusion in citing a compound species without a varietal name, then the abbreviations cpd sp. may be added. Thus remarks on *C. Petriei* cpd sp. would be understood to refer to both varieties.

With increasing numbers of jordanons more complex compound species occur, and it may become a matter of opinion whether a particular jordanon should be included as a variety of a compound species or receive specific rank. Also it may sometimes be a matter of opinion whether two jordanons are clearly enough differentiated to receive independent varietal rank or should be united to form a compound variety. In no scheme can the personal equation be altogether eliminated. In the compound species *Hebe salicifolia* there are a great number of jordanons, and one—var. *Atkinsonii* (a compound variety)—is so distinct from all the other jordanons that our chief reason for retaining it in the compound species is that it may prove to be the type of Forster's original *Veronica salicifolia*. Indeed the senior author had treated it as a separate species until ecological observations throughout its area of distribution had revealed the possibility just mentioned. Obviously varietal names of this kind are of the utmost importance. It is worthless, for example, for a collector to cite *Hebe buzifolia* as occurring in a particular locality, without reference to the jordanon or jordanons that are to be found there. If no name be available (and such must be the case very often for many a year yet) he should give a description of the group he is dealing with.

An unstable form due to environmental influences, and changing from the usual ("normal") form when these influences are sufficiently modified we call an "epharmone." Of course the "normal" form is as much an epharmone as any other, and in some cases, it may be, of the different environmental forms none so predominates as to deserve the title "normal." Our floristic term "epharmone" thus corresponds to some extent with what Clements (12, p. 155) from the ecological side refers to as an "ecad," but the taxonomist is not required to analyse in detail the various factors which by their combination produce the "epharmone"; he is concerned with the resultant form. Hooker's var. *prostratum* of *Leptospermum scoparium* is, according to our usage, an epharmone, not a variety. Where it is useful to give names to epharmones, or where varietal names have wrongly been given to such we would cite them as, e.g., *L. scoparium* eph. *prostratum*. Into the vexed question whether an epharmone ever becomes so fixed as to result in the formation of a jordanon (heredity of an acquired character), we need not here enter. It is sufficient for the taxonomist and descriptive ecologist to know the status of his forms as they exist at the present time.

Where hybridisation takes place—and New Zealand evidence very strongly suggests that this occurs far more freely in nature than is generally supposed, and that the hybrids are by no means infrequently fertile—diversity of a still more complicated character is found. This hybridism is not confined to jor-

danons within a compound species, but jordanons of most distinctly separated species may cross, and inter-generic hybrids are not unknown. The extreme members of such polymorphic groups have often been united in floras under the designation of a single species, on the grounds that the various "intermediates" are "passage-forms" linking together the extremes; and the "species" so constituted is spoken of as "variable." Another common procedure has been to treat the hybrids coming about midway between the parents as a distinct "species." Such a polymorphic group with its jordanons, epharmones and hybrids we call a "linneon," thus making the term more definite in application than Lotsy (46, p. 27) who defined the *Linneon* as designating "a group of individuals which resemble one another more than they do any other individuals." Thus the "species" *Olearia arborescens* as diagnosed by Cheeseman (10, p. 919) is a linneon made up of (1) three groups of jordanons so distinct from one another as to be better treated as separate compound species—*O. arborescens* sens. strict., *O. Cheesemanii* (= var. *angustifolia* Cheesem.), *O. capillaris*; (2) hybrids between certain of the jordanons and some of the hybrids between these and *O. ilicifolia* or *lacunosa*; (3) certain epharmones, e.g. of *capillaris*, and probably "var." *cordatifolia* T. Kirk—a shade epharmones; (4) certain as yet undescribed jordanons and hybrids. The whole linneon thus consists of a so-called type "varying" from a divaricating-shrub with leaves about 7 mm. long to a canopy tree with leaves up to 10 cm. long, by way of a multitude of "intermediate" forms; and of this linneon¹ Cheeseman states, "Perhaps the most variable species of the genus, but generally to be recognized in all its forms by the thin white and peculiarly satiny tomentum on the under-surface of the leaves"! When the herbarium method can lead such a painstaking and skilled worker as Cheeseman to such lengths, we may be excused for thinking that that method has served its day, and outlived its usefulness. Such a name in any case is worthless for ecological research.

Where we do not know—a frequent circumstance—or where we find it convenient for the time being to waive the status of an individual or a group we use the term "form." Where a "species" has been founded on garden material of unknown origin we remove it from the flora and apply the term used by Bailey (6, p. 25) "cultigen." There are at least 15 of this class accepted by Cheeseman in the *Manual*, mostly in the genus *Hebe*, so widely cultivated in gardens. *Nothopanax Macintyreii* is described from a single plant growing in a garden. Not only is its place of collection unknown, but from the description it appears to be a hybrid and it matches one of the hybrid swarm *Nothopanax Colensoi* × *simplex*. To include such cultigens as valid species of the flora seems to us a practice essentially vicious.

¹ This "species" is an excellent illustration of that misuse of authors' names permitted by the *Rules of Botanical Nomenclature*. Thus in the *Manual* the authors of the name in Cheeseman's sense are given as Cockayne and Laing whereas their species includes only *O. arborescens* proper, and excludes *O. capillaris* and other groups included by Cheeseman.

The term "type"—now so greatly in evidence—we restrict to its proper usage as stated by Diels (35, p. 73), "Wer eine Pflanze neu beschreibt, ist verpflichtet, sein Original als solches kenntlich zu machen, da es für immer der Beleg für seine Beschreibung bleibt. Die Herbariumpraxis nennt ein solches Original 'Typus.'" Considering the surprising ways in which the term "type" is frequently used in floristic botany it is not superfluous to draw attention to the matter. Sometimes what is merely the most common form is referred to as the type, at others merely that which is best known to the writer, or even that which he first learnt to recognise as belonging to the species in question. A specimen may be spoken of as having been compared with the "type" when what is meant is merely that it has been compared with other specimens from the country in which the type was collected. The name *Epilobium junceum* as usually treated by New Zealand botanists refers to a linneon. Solander gave the name to specimens he collected near Gisborne, but his name was not published. Forster applied the name to specimens he collected, probably, at Queen Charlotte Sound, but published no description. The first valid publication of the name was thus that of Sprengel in 1825¹. The material used by Sprengel is therefore the type material and not as Cheeseman (10, p. 603) appears to consider, that originally collected by Solander.

5. METHODS OF PROCEDURE.

It will be obvious from what has gone before that we advocate no undue haste in either "creating" or "rejecting" species and varieties. The many compound species and linneons in the New Zealand flora provide material for an army of workers, and collectors will do far greater service in skilfully collecting and studying even the commonest and most "well-known"—frequently very badly known in reality—species, than in hunting for scraps of "something new." We fear that Hooker was unduly optimistic when in 1853 (41, p. xiv) he said "The time however is happily past when it was considered an honour to be the namer of a plant," and certainly collecting merely in the hope of having a plant named after one is not yet out of fashion! We hope the methods here outlined will prove of service to those collectors who have passed the stage of looking for "new" species, or ransacking herbaria for scraps of "puzzling plants" and who desire to do really useful work but are not altogether sure of what such consists in.

(a) *Work in the Field.*

The quantity and quality of the work possible of accomplishment are subject to obvious limitations—time available, accessibility of the locality, state of the weather, season of the year, and so forth—and only general

¹ We are greatly indebted to Prof. W. Wright Smith for sending us a copy of Sprengel's description.

principles can here be set forth, which must be modified according to circumstances¹.

Equipment. The equipment required for profitable work is not excessive, though a full list might at first sight appear formidable. The following are essential: (a) a roomy rucksack (preferably with side pockets), a supply of handy-sized tins (the flat, round-edged cigarette tins of "fiftys" and "hundreds" are excellent, and mustard tins are good also), collecting portfolio—a convenient size is 35 × 25 cm. (two pieces of stout cardboard with newspaper between will suffice, though more elaborate articles may readily be designed), stout knife (a good sheath knife is excellent for many purposes), measuring tape (the 1 m. or 2 m. steel tapes in metal covers are good), small film camera for photographic "notes"; (b) Notebook and plenty of pencils. The notebook rather thin and of handy pocketable size, with stout cover, and should be provided with a light waterproof wrapping to ensure safety in wet weather. We find the ordinary "garden" pencils excellent for field purposes, especially in rainy weather. A small notebook for wet weather, from which the notes can be transferred at convenience is a great assistance at times². A plentiful supply of small nurserymen's labels with string attached, and a ball of string.

Useful, and in some excursions essential, equipment includes also a compass, an aneroid barometer, a digger (we find a bricklayer's hammer with the hammer head transformed into a pick point, and with a stout handle—the New Zealander will find a matured branch of *Shawia paniculata* is excellent—exceedingly useful for collecting in stony ground), maps in waterproof covering. Of course where a base camp can be established much more may be taken with advantage—stand camera of at least quarter-plate size, large plant press, field glasses, and what not.

But as Tansley says (53, p. 80) "the map, notebook, sharp eyes and a wide-awake mind are the only essentials." At least, no amount of "gear" will prove a substitute for these. A good pocket Flora is no doubt highly desirable, but for the New Zealand botanist there is at present none available, though "Cheeseman," despite its good 2 kg. weight, may go as far as the base camp.

Collecting. Here the "sharp eyes and wide-awake mind" are eminently to be desired. Preliminary study of the literature available, if there be any such, concerning the locality, may help to reveal the problems likely to be met with. Before actually collecting a brief description of the association should be drawn up, one's power of rapidly recognising the special features improving with practice. The collector should aim at being able rapidly to take intelligent notes. He will have to decide the most profitable course to take—whether to concentrate on a few, or even one of the problems presented and gather

¹ Useful information may be gleaned from Tansley (53), Tansley and Chipp (54), Markgraf (48) and Rübel (52).

² Note taking in rain is most unsatisfactory, but at times unavoidable. This is one reason for recommending *thin* notebooks, as otherwise a book full of important notes may be ruined.

material to elucidate it, or to endeavour to collect material concerning all the problems he recognises to be present. Where the locality is such that the collector is not again likely to be able to visit it, and the chance of other visitors studying it is also remote, it may be better to deal with the vegetation rather broadly, collecting freely. Where plenty of time is available, or where further opportunities of visiting the locality are certain to occur, it may be better, after a preliminary survey, to proceed in detail with a particular problem. In any case, with practice, a surprising amount of good collecting may be done, especially if the excursion is composed of several members who may divide up the work among them. But this rarely happens in New Zealand, and the ecologist must accustom himself to solitude and self-reliance.

We will imagine that the collector has reached an example of *Hebe* shrubland, and has decided to concentrate upon it. After a general reconnoitre he may find that he cannot give a name to any species present (though a year or two ago he would have bestowed names with all confidence). He therefore proceeds to give temporary names for what he decides are the jordanons present—those forms which appear in plenty of very closely similar characters, carefully notes the nature and amount of polymorphy present, collects his specimens to give in miniature a picture of the plants composing the association. No more than *one* good specimen is taken from any plant. To this specimen is attached a nurseryman's label which gives its number and habitat, and in the notebook, under the same number, any important details that the specimen does not reveal are at once recorded. Thus, if 16 specimens have been taken from habitat *A*, the labels and notebook numbers run from *A* 1 to *A* 16. To prevent confusion with subsequent collectings the date should also be attached. Thus the labels read: "9/XII/26 *Hebe* swarm *A* 10," etc. More elaborate methods may be evolved by the experienced collector, but the above will allow even the novice to do serviceable work. Indeed both for expert and novice time may not be available even for this amount of detail, *but so long as not more than one piece is taken from each individual, and all from one group are tied together with the habitat label*, further labelling can be left till the base camp is reached, when the bundles may be wrapped in sphagnum or the best substitute available, so that they may reach the garden in good order for planting. Then also pieces of each can be made into herbarium specimens. If flowers or fruit are present, duplicate specimens may be placed in the tins or the collecting book. But this needs exceeding care to see that the labels correspond to those of the bundles, and that they do not get displaced. Carelessly or hastily collected duplicates are worse than none at all, and if, later, there is the slightest doubt they should be cast aside, and so with plants in the garden the labels to which have been displaced.

Thus material will have been gathered that will provide real, if incomplete, information, from which definite knowledge as to the jordanons, hybrids and epharmones present can be gained. The method can of course be applied to

forms of any genus, whether hybridism is found to be occurring or not. No longer, with such methods, would ill-founded "new" species be made from random scraps that happened to take the eye in passing or, worse, from such scraps in existing herbaria. There will also be material both for growing and the herbarium.

Where a worker has the good fortune to have a valuable community within easy and constant striking distance, a further great advance towards the solution of field taxonomical problems may be made, by the permanent labelling of selected wild plants. A good example—the first, so far as we know—of the value of this is the work accomplished by Messrs G. Simpson and J. S. Thomson. In their study of a remarkable *Hebe* community near Dunedin in which occur *H. salicifolia* var. *communis*, *H. elliptica*, and a wonderful series of hybrids between them, they have carefully selected certain wild plants and permanently labelled them with copper discs. From these selected plants cuttings have been distributed to us and to others, so that material, the first of its kind, is at hand for a detailed study of the taxonomy of the group. A glance at our paper revising the genus *Hebe* (25, p. 20, under *Veronica amabilis*) will reveal the great importance of a study of the taxonomy of this group. Similar work may be urged upon our institutions that have an opportunity to carry it out. Almost alongside the Mountain Biological Station of Canterbury University College at Cass, for example, lies waiting a remarkable *Hebe* community of which we have but scanty knowledge, but which would repay the closest investigation. So too the Otago University has great opportunities for the study of the polymorphic groups of *Cassinia* and other genera on the easily reached Mount Maungatua and Flagstaff Hill.

(b) *The Herbarium.*

There are of course many different grades of herbaria, constructed on diverse plans and with diverse ideals, ranging from the small private herbaria, dealing it may be with one particular group of plants, or a special locality, to the great national herbaria. The great majority have been built up from the taxonomic standpoint, but of recent years attempts have been made to construct herbaria on ecological lines¹. Clements (11, p. 329) has discussed the construction of herbaria on synecological principles, especially "Formation and Succession" herbaria, and has illustrated his conceptions by reference to a herbarium built up to give a picture of the plant formations of Colorado. Yapp (61, p. 14) deals with the possibilities of herbaria formed on autecological principles, using the term "Ecological reference herbaria." Both these types are eminently desirable, and as Yapp suggests would give valuable opportunities for team work.

The herbaria we have in mind, however, which might be termed "eco-

¹ As we write Dr G. E. Du Rietz, at present in New Zealand, is collecting specimens for the University of Upsala to represent the plant formations.

logical-taxonomic" herbaria, while giving a picture of different aspects of a community, are constructed mainly to suit the needs of the ecological or field taxonomy we advocate. We attempt to bring together suggestions derived from field-work, which has revealed the great weaknesses in existing herbaria of all grades. These weaknesses may be summarised as: (1) failure to recognise the fundamental importance of field evidence as to the status of the individuals concerned—the jordanons, hybrids and epharmones; (2) utterly inadequate representation, in most cases, of the material present in the field; (3) very insufficient documentation of the specimens, as already discussed; (4) lack of reference to the detailed information that should be found in the field notebook; (5) insufficient attention to the matter of type specimens of newly described species; (6) lack of really adequate precautions against misplacement of labels during the various stages from gathering to final laying-in, and against mixing of specimens during these processes, or during subsequent examination.

To remedy this state of affairs we suggest: (1) Field study, collecting and labelling on the lines already given; (2) the grouping together under locality and habitat covers of the specimens collected for each species, etc.; (3) the adoption of sheet tickets showing in addition to locality, habitat, altitude and collector's name, the following data—(a) botanical district; (b) the nature of the plant community, the names of other species of the same genus in the community or its immediate neighbourhood; (c) the growing place of the individual from which the specimen was taken; (d) statement of the status of the specimen as far as ascertained, with reference to the number and page of the field notebook where details are given; (e) the placing of specimens from *only one individual* on any one sheet; (f) statement of the individual species notebook where further information is given as to the species in general; (4) the permanent retention of the field label, so fixed as to remove under ordinary circumstances any possibility of displacement. The notebook for the individual species, just referred to, we confess we have not yet properly adopted ourselves, but we have become convinced of its great utility. In it will be recorded important details concerning observations on the species—its morphology, range, new localities, etc., epharmony, hybridism and so on—with cross-references to the herbarium sheets, garden cultures, field notebooks, drawings, photographs and published information.

Herbaria constructed on these lines will naturally involve a great amount of detailed work, but unless such is performed the herbarium specimens will have little or no value.

Individual private workers might do well to concentrate on special groups, and collectors not aiming at themselves establishing herbaria could distribute their material accordingly. The great herbaria, e.g. that of Kew, aiming at world-wide collections, are very largely dependent on outside collectors, and the value of the work they can accomplish will depend upon the adequacy of the collecting. In many cases the collector must, perforce, be

content with something less elaborate than workers settled in a country can accomplish, but just so far as their work is based on sound principles will it be of value. Herbaria constructed on the lines we advocate would at once cause the student to realise that to describe "new" species from a few scraps that give no indication at all of the range of forms found in the locality from which they were collected is a vicious practice.

The far-reaching results of the new taxonomy are strikingly illustrated by our revision of the genus *Hebe* (25, p. 1), although we were hampered right and left in dealing with herbarium material, etc., by the weaknesses above referred to. Cheeseman (10, pp. 778-783) lists 86 species (as *Veronica* section *Hebe*). Of these we reject 20 on various grounds. Apart from synonyms¹ we consider only 70 of the hitherto described species to be valid, and even of these we think at least 8 are under grave suspicion. We reject 13 as being based on hybrid material, 10 as being cultigens, and 6 as being described from altogether insufficient material for any determination as to status being made. Similar statements hold good for many of the described "varieties." On the other hand we have been able, using the ecological-taxonomic method, to describe a number of distinct jordanons either as species or varieties; while by the herbarium method we could have made dozens of new species, supported by apparently most convincing specimens.

Craib (29, p. 237) suggests that young men going into the overseas forestry or agricultural service might receive six or nine months' training "in one of our larger herbaria spent in the routine work of sorting out and laying-in specimens and finally in systematic work either general or restricted to some particular genus." We are distinctly opposed to this. We would, on the contrary, have the young man trained in the field so that he would be free from prejudice and would learn to collect material for Kew, etc., as it ought to be collected. Otherwise his outlook would almost certainly become wrongly orientated.

(c) *The Experimental Garden.*

Essential for the purposes of the new taxonomy is the establishment of carefully controlled experimental gardens. The garden serves the following purposes: (1) Material corresponding to the herbarium specimens may be grown for further investigation of the status of individuals, and to serve as material for description of details not shown by the living plants when collected, or for which time was not available. Specimens not in flower may be grown to the flowering and fruiting stages; specimens suspected of being epharmones may be subjected to various environmental conditions. (2) Different forms

¹ Cheeseman's conception of what constitutes a synonym is often at variance with ours. Thus (10, p. 790) he cites var. *communis* as a synonym of the "type" of *H. salicifolia*, but var. *communis* does not, as far as we know, occur in North Island, is almost certainly not Forster's type, and, type or not, each variety, according to our usage, should have a name. Nor does his general description fit the jordanon *communis*, but refers to a mixture of forms.

may be grown together for comparison in the living state at close quarters. (3) Pure cultures may be made. (4) Suspected hybrids may be investigated more fully and seed secured from them under controlled conditions. (5) Hybridisation experiments may be carried out to ascertain whether putative parents produce hybrids resembling the supposed hybrid forms found wild. Finally (6) the same material can often be grown by many workers living in different localities.

To illustrate the uses of the garden we may refer to the following examples. As described in the *Manual*, ed. 1 (9, p. 713), *Astelia nervosa* is a linneon, of which a variety *montana* (of which *A. Petriei* Ckn. is considered a synonym) is given. In the *Manual*, ed. 2 (10, p. 317), *A. nervosa* is still a linneon, but the distinct species *A. Cockaynei* (\times *A. nervosa* var. *montana* of ed. 1, in part) and *A. Petriei*, both based on extensive field evidence supplied by the senior author, are accepted. Further ecological research has shown that *A. nervosa* proper is a compound species made up of the distinct jordanons var. *grandis* and var. *sylvestris*, and probably others. Research has also shown that var. *sylvestris* hybridises with *A. Cockaynei* giving the "intermediates" that caused Cheeseman at first to consider the latter as coming under *A. nervosa*. Now, in the senior author's garden *A. Cockaynei* has been grown for ten years without in the least approximating to *A. nervosa* var. *sylvestris* of the same neighbourhood. Side by side with the above plant of *A. Cockaynei* has been grown for the same period the subalpine shrubland *Astelia* of Mount Egmont, which closely resembles *A. Cockaynei*. This, however, has changed markedly in appearance, coming much closer to *A. nervosa* var. *sylvestris*, but is by no means identical with it. In the junior author's garden this change was seen to commence during the first year after transplanting. The exact status of the Mount Egmont subalpine plant thus remains undecided, and can be determined only by the study and cultivation of all forms of *Astelia* growing in the Mount Egmont subalpine forest and shrubland. But we now know that it is *not A. Cockaynei*, as we first supposed. Had we not grown this form, herbarium specimens, even if copiously collected, would not have given any suspicion that our first supposition was incorrect, especially considering the obscuring of important details that occurs during drying and pressing. Diels (35, p. 173) also strongly emphasises the value of the experimental garden to the taxonomist in testing whether the forms found belong to jordanons, epharmones or hybrids, though he does not use these particular terms.

6. EXOTIC SPECIES.

Nearly 40 exotic species are included by Cheeseman in the New Zealand flora, although in many cases he was aware of their true status. As justification of this procedure he remarks (10, p. 532) in reference to *Geranium molle*, "There can be little doubt that this is introduced, but as it has had a place given to it in previous works on New Zealand plants, and as it is now found in

all soils and situations, and would certainly be considered indigenous by a stranger unacquainted with its history, it appears best to retain it in the Flora." In other cases, e.g. *Imperata arundinacea* var. *Koenigii* (10, p. 136), he gives the species "the benefit of the doubt"; in others again, while himself having no doubt of the exotic origin (e.g. *Cyperus vegetus*—p. 215) he retains species because previous workers have described them as indigenous.

Were his reasons in all cases strictly accurate—*Geranium molle*, e.g., is certainly *not* found "in all soils and situations"—we do not consider them at all cogent, and in another paper (26, p. 61) we have listed all the species we consider should be removed from the flora, and those concerning which further investigation is desirable. No matter what may be considered the best procedure in long-settled countries, where origins must in many cases be no longer determinable, we consider that in New Zealand and similar countries, where the primitive and semi-primitive vegetation still occupies the most prominent position, and where from historical and other reasons there are really few cases in which there is any doubt, Cheeseman's practice was most unfortunate, especially as it is followed religiously—particularly in "popular" publications—by those who refer to no other writings. In view of the important phytogeographical principles involved, and of the far-reaching conclusions sometimes drawn from the presence of "wides" in a flora, we take the contrary stand, and would prefer to exclude doubtful cases, rather than give them "the benefit of the doubt."

Here we may refer to the fact that recent workers have tended to create or restore vicarious species that had previously been included in larger groups, thus often making an endemic species out of what was before considered a "wide." Thus for New Zealand the following, among others, have been separated from the bracketed species—*Centella uniflora* (*C. asiatica*), *Myosurus novae-zelandiae* (*M. aristatus*), *Elatine gratioloides* (*E. americana*). While, in general, this tendency appears to be sound, we would emphasise that before a decision can be arrived at ample and properly collected material is necessary. This is especially true in the case of compound species. From the specimens we have seen we consider *Hebe elliptica* of subantarctic South America to agree very well with one of the jordanons of that compound species appearing in New Zealand. But a worker merely in possession of specimens of another jordanon might well consider the plants of the two countries to be specifically distinct. There are a number of other New Zealand species awaiting proper investigation from this point of view, e.g. those hitherto referred to *Avicennia officinalis*, *Gratiola peruviana*, and *Hierochloe redolens*.

Other species that need investigation are those in which it seems possible that we have in New Zealand both indigenous and exotic representatives, e.g. *Solanum nigrum*. The importance of adequate study of these matters may be illustrated by reference to the case of the fescues. The identification of our New Zealand forms is mainly due to Hackel, who had very wide views as to

the contents of various species. Cheeseman (10, p. 206), on Hackel's authority, admits *Festuca rubra* to the flora, saying, "It has considerable value as a sheep-grass [really it has very little], and is often sown on sheep-runs. From that fact it is doubtful whether some of the European forms that can now be readily collected even in remote districts may not have been introduced. Of some varieties, however, there is no reason to doubt their nativity." But of these "varieties" neither diagnoses nor localities are given, and further, it is certain that a great deal of hybridisation has occurred. Here is therefore a case where the task of arriving at the status of the various forms is one of great difficulty, if not of impossibility. To us it seems that only those forms which research shows to be jordanons not occurring in other countries should be admitted to the flora. And it is obvious that no collection of herbarium specimens, however complete, could be satisfactorily determined by any specialist however expert, without the added information derived from field studies and experimental cultures.

7. AN ACCOUNT OF THE VARIOUS TAXONOMIC GROUPS.

(a) *The Individuals.*

As already emphasised the goal of taxonomy is the power to discover the status of the individual plant. Plant after plant has to be compared and the eye trained to recognise similarities and differences—the student of *Hebe*, e.g., has to develop the "Hebe eye." Of paramount importance is the recognition of the jordanon and the tracing of diversity to its causes. This is not the work of one season, but of many. No better training can be recommended to the tiro than the minute study of the forms occurring in a locality of restricted area. At this stage specific names may be more of a hindrance than a help, as the tendency may then be to fit the specimen to the name, rather than to find out what the field evidence is as to its nature. Such close study will be far more valuable than the gathering of specimens for some "expert" to name, or the poring over herbarium material of doubtful origin and character.

(b) *The Simple Species.*

Simple species are those that contain but one jordanon. We also treat as simple species those in which detailed research may reveal the existence of more than one jordanon, which, however, are not capable of separation by any diagnoses of a clear-cut nature. Such, one might say, "microscopic" jordanons are of immense interest to the geneticist, but the time is not yet ripe for their utilisation for taxonomic purposes. It may sometimes happen that a species may be simple in one country, but compound in another, or at least represented by a different jordanon. Thus the var. *australiensis* is the only jordanon of *Juncus maritimus* known to occur in New Zealand. As already mentioned the tendency of recent taxonomy has been to treat such jordanons as distinct species rather than varieties of a compound species. The

jordanon once recognised, the question of giving it varietal or specific rank will often depend for its answer upon the taxonomist's views as to "lumping" and "splitting." One cannot lay down a definite rule as to when a particular jordanon is of sufficient grade of distinctness to be treated as a species or not. To some a wide conception of compound species will appeal, to others the reverse. For instance, should *Azolla rubra* be treated as a variety of *A. filiculoides*? The first point is to decide whether we are dealing with two jordanons or not. Assuming that we have been able to decide that we are, then it might be argued that the varietal treatment helps to bring out in clearer light the phytogeographical relationships between South America and New Zealand. On the contrary it might be urged that this relationship would be over-emphasised. To us, in the present stage of our knowledge of plant distribution and evolutionary history, it seems preferable to emphasise the distinctions of the jordanons of different countries, as thus there will be less likelihood of facile and over-hasty generalisations on matters of which we have really but exiguous information.

There are, however, in the New Zealand flora itself, certain simple species that stand out perfectly distinctly from any other group. These jordanons, therefore, do not require a varietal name. Thus we have the simple species: *Agathis australis*, *Epilobium pernitens*, *Aciphylla Hookeri*, *Hebe Gibbsii*, and so on, each most clearly marked off from all its allies. A striking example of a simple species becoming "artificially polymorphic" is *Epilobium nummularifolium*, described by A. Cunningham (31, p. 31). Hooker (42, p. 77) united with it others of A. Cunningham's species, and this course was followed by subsequent taxonomists—all using the herbarium method. Cheeseman (9, p. 180) says of the linneon thus created, "An excessively variable plant. The varieties described above are simply prevalent forms, and pass into one another by insensible gradations"—the "species" still being cited as of Cunningham! Later, however (10, p. 609), principally owing to the ecological work on the group by the senior author, Cheeseman reverted to Cunningham's treatment, giving in addition the three (and there are more) true jordanic varieties established by Cockayne (22, p. 171). *E. nummularifolium* itself occurs throughout New Zealand, is recognisable at a glance, is perfectly invariable except for small epharmonic changes, and at present is not certainly known to hybridise. Further it is far from being ecologically equivalent to *E. pedunculare*.

(c) *The Compound Species.*

The majority of New Zealand species are compound, i.e. are made up of two or more jordanons. We have already referred to the difficulty that may arise as to whether a particular jordanon should be attached to a compound species as a variety or treated as a separate species. Although we have stated that for jordanons of different countries it is usually better, at present at any rate, to treat them as species, for those of a single country we unhesitatingly

consider that relationships are usually better expressed by grouping together as jordanic varieties of a compound species such jordanons as are clearly closely related in a number of characteristics. Each jordanon of such a compound species must have its varietal name, including the type. Where the whole compound species is referred to, and it is essential to indicate that we are not dealing with a simple species we may cite the species as, e.g., *Hebe buxifolia* comp. Where there is no danger of misinterpretation this abbreviation may be omitted. Where a particular jordanon is being dealt with this must be fully cited, e.g. *Hebe buxifolia* var. *pauciramosa*. This is a matter at present far too much neglected in floristic lists, the value of which thus becomes minimised, for related jordanons may require different growing places. We have already shown that to establish a compound species on the usual herbarium lines is impossible, but we may give another illustration. Bitter (7, p. 246 *et seq.*) made an elaborate analysis of the New Zealand forms of that most complex genus *Acaena*. But his work, necessarily largely based on inadequate herbarium material—he also uses cultigens—is suggestive merely. Field observations and garden cultures by the senior author (e.g. 19, p. 193) have gone some way towards providing an analysis of various species on natural lines.

Since many compound species are known to produce inter-jordanic and inter-specific hybrids, their analysis becomes a work of great difficulty, and progress to be of value must be cautious in the extreme. It thus happens that in the *Manual* (10) we find compound species in which the “varieties” fall into two classes—(1) those founded on herbarium material only, and (2) those founded on the new taxonomic conceptions. An example of the first is *Deyleuxia Forsteri* (10, p. 158). The first variety given is var. *pilosa*—a distinct jordanon (or perhaps group of jordanons), but so markedly distinct (*pace* Cheeseman, who says, “Hardly more than a luxuriant state of the type”) that it is better treated, as by Buchanan, as of specific rank. Of the remaining 5 it is possible that var. *littoralis* and var. *micranthera* represent jordanons or groups of such, but of the others there is altogether insufficient evidence as to their status. Thus the whole group of forms is badly in need of investigation. An example of the second is *Epilobium pedunculare* (10, p. 610). For this there are given 3 varieties, each from field observations and experimental culture known to represent distinct jordanons.

There are of course all grades of complexity in compound species. Some may have few jordanons, and these differing in but few characters, others may have many jordanons, and these differing in many characters. *Geranium Traversii* has two jordanons, the one with pink, the other with white flowers. *Linum monogynum* has probably several white-flowered jordanons, and also one at least—var. *chathamicum*—with the petals flaked with pale blue. *Forstera sedifolia* has a white-flowered, and a dark “eyed” jordanon—var. *oculata*. The *oculata* form is also to be found in the allied species *F. Bidwillii*.

Of more complex compound species there are sufficient examples given in various parts of the paper.

Coloration phenomena sometimes assume taxonomic importance. In the various jordanons of *Cyathodes acerosa* there are forms with white and forms with red "berries." In *Pseudopanax crassifolium* var. *unifoliolatum* forms occur in which there are distinctive colours possessed by the mid-ribs and under surfaces of the leaves. There is some field evidence that this may be connected with distinct jordanons. But that this must not be too hastily assumed in any particular case is shown by the fact that in several trees studied by the junior author it was found that the purely juvenile long leaves had dark red mid-ribs and chocolate under surfaces. As older and older leaves were examined there was found a transition of mid-ribs through yellow to the yellowish green of the adult leaves, of under surfaces through dull grey to the lightish green of the adult leaves.

A matter that as yet has had insufficient attention paid to it in New Zealand in connection with taxonomy is that of phenology. Certain species of *Hoperia*, e.g., are distinguished, among other things, by possessing very different flowering periods, but very much more remains to be found out. A study, for instance, of the flowering periods of the forms of *Hoheria sexstylosa* and *Hebe salicifolia* would yield much valuable information. Some appear to have long periods of blooming, others short, and blooming occurs at different periods.

How far certain distinct apparently true-breeding forms are due to parthenogenesis or apogamy, using these terms in the sense of Winkler (60, p. 1), we have no information, but it is unlikely that such cases will not be found to occur in New Zealand. We refer to the matter only to draw attention to the need for investigation. For ordinary taxonomic purposes such "races" present no difficulties, as they remain constant, and for purposes of description and identification may be given distinguishing names.

In connection with compound species the matter of "ecotypes" needs brief consideration—a full discussion would lead us too far from the main purpose of this paper. Turesson (55, p. 172) says, "When it is found that the Linnean species is made up of a great number of hereditary forms, and when it is further established that such hereditary forms are found in nature to be grouped into different types, or rather complex-types, confined to definite habitats, the necessity of an intensive study of the Linnean species and their habitat types or races, becomes pressing." These "hereditary habitat types," "arising as a result of the differentiation of the species-population in response to particular habitat conditions" he terms ecotypes. In a further paper (56, p. 147) he gives a number of illustrations of ecotypes, e.g. for *Artemisia campestris* he describes *dune, field and meadow* and *alvar* ecotypes. In a suggestive treatment of "parallel ecotypes" he names various ecotype groups, e.g. *campestris, arenarius, alpinus*.

Now, while it may be urged that none of Turesson's cultures have been of

sufficiently long duration—the earliest cited began in 1919 and were recorded for 1924, whereas Cockayne (17, p. 18) has shown that a shrub that had remained prostrate for eight years, then began to assume the erect form—definitely to rule out the possibility of certain of his ecotypes being long-persisting epharmones; that it is perhaps premature to speak of the types being definitely hereditary when no data are given as to the behaviour of the offspring, and that the possibility of parthenogenesis in several genera, e.g. *Hieracium*, *Leontodon*, is not reckoned with, we fully expect that further work will prove the conception of ecotypes to have considerable value. We cannot see, however, that there is any the less need for the field botanist to make the deepest possible analysis of his material. As Cockerell (28, p. 588) says, "Thus, while the ecotype system is highly illuminating, it should not take the place of definite names accompanied by precise descriptions, and supported by type specimens in the herbaria. Also, it is not clear that the most minute analysis of the various biotypes will not after all furnish the necessary materials for an adequate synthesis." To consider a few New Zealand cases. *Acaena novae-zelandiae* has a var. *pallida* confined as far as is known to sand-dunes, and there is a dune-dwelling jordanon of *Geranium sessiliflorum*. *Astelia nervosa* has a var. *sylvestris* confined to forest, and a var. *grandis* of lowland swamp. *Senecio lautus* has coastal, lowland and montane jordanons, and there is much epharmonic change also. In other cases the jordanons are separated in geographical rather than habitational or associational distribution. *Arthropodium candidum* has a jordanon apparently confined to a restricted area, and another that is widespread. Both grow under similar habitat conditions. So too *Danthonia Raoulii*, as growing in subalpine grassland on Mount Egmont has a very distinct appearance from that of the jordanon of the Volcanic Plateau Botanical District. The northern jordanon of *Leucopogon fasciculatus* is distinct from that found further south under apparently similar conditions, and so on. Many jordanons may be found unchanged, except epharmonically, in diverse habitats, e.g. *Cordyline australis*, *Lobelia anceps*.

The point we stress, however, is that most distinct jordanons may grow side by side, e.g. in *Geranium sessiliflorum*, *Acaena Sanguisorbae*, *Melicytus micranthus*, *Leptospermum scoparium*, *Epilobium melanocaulon*, *Myosotis pygmaea*, *Phormium tenax*, *Gentiana serotina*, *Coprosma Petriei*—to name a few.

Again there are many compound species the jordanons of which cut across these divisions, and in New Zealand there lies ahead much intensive work before any far-reaching conclusions can be drawn from the distribution of the jordanons in nature. In a word the ecotype conception does not at all free us from the necessity of first sorting out the jordanons.

(d) *The Epharmones.*

We coin the word *epharmonie* to express a taxonomic conception, and by it we understand the growth form of an individual in relation to its growing

place. It must be emphasised that we apply the term irrespective of what may be the status of the individual—jordanon or hybrid. In most cases there is a prevailing form, often spoken of as the “normal” form, which has—it may be—come to be looked upon as representing the true character of the jordanon, if we are dealing with such.

The less usual forms are those generally referred to as habitat modifications—Clements’s “ecads,” Turesson’s “ecophenes.” But not only the more unusual, but also the “normal” is a habitat form—an epharmone—and in some cases no one epharmone is strikingly more abundant than another, and it becomes impossible to refer to a “normal” form, meaning thereby a predominant form, nor is there anything “abnormal” about any epharmone, if “abnormal” connotes, as it usually does, “unnatural.” All the epharmones that a particular jordanon is able to assume must be included in the conception of that jordanon, and according to our usage the term *variety* cannot be applied to these inconstant forms, but must be restricted to true-breeding races¹. Whether certain forms that now fulfil the requisites of *varieties* (jordanons) originated by the fixing of originally habitat-induced characters or not, need not be discussed here. Only forms now capable of alteration with sufficient modification of habitat are our epharmones. Where it is considered desirable to give special names to epharmones they could be cited as, e.g., *Lobelia anceps* eph. *scandens*, but in general it appears better not to give epharmones names, as these might easily be misinterpreted as varietal, and so lead to a conception opposite to that which was intended.

“Abnormalities” due, e.g., to fungal or insect attack concern the taxonomist in so far as they may tend to be mistaken for varieties—in a wide sense they might be included under the term “epharmane.” Such forms are in general somewhat easily recognised, and are little likely to cause confusion, unless the whole plant is involved. That they cannot be left out of consideration by the taxonomist is illustrated by the case of *Discaria toumatou*. The senior author (23, p. 332) referred to the discovery of two adult flowering bushes, semi-juvenile in form, of which he received ample living specimens. “The twigs are slender, drooping, and not stiff, the spines are more or less soft and the flowers comparatively few. The plant might well be considered as a form growing under conditions of especial shade and moisture in the air, yet the two bushes are side by side with the usual intense xerophytic form of the species.” When, however, he was able to examine one of the plants *in situ* he saw the folly of his premature conclusion and over-haste (24, p. 206) in that the whole plant was a “witches’ broom.” Later, however, he discovered a true jordanon matching these forms. The junior author has seen a number of plants growing together, which were of rather dense cushion form, practically without spines. In the neighbourhood was a community of the usual semi-

¹ The term “variety” in the *Manual* (10) has the loosest application, and includes jordanons, mixtures of such, epharmones, mixtures of such, hybrids, and quite good simple species.

divaricating spiny form. These cushions were found to be due to the constant browsing of rabbits.

On the other hand we should not too hastily decide that an unusual is an abnormal form. Concerning *Olearia nummularifolia* var. *cymbifolia* Kirk (45, p. 273) has the curious remark: "var. *cymbifolia* appears to be a depauperated condition, largely caused by the ravages of insects; it produces few flower-heads, and the upper leaves are greatly reduced in size." Field observations lend no support whatever to this idea, and the variety is a most distinct jordanon, better treated, as by Cheeseman, as a species apart from *nummularifolia*. The teratological field has, however, been neglected in New Zealand, and deserves full investigation.

Turesson (56, p. 231) recognises the confusion that epharmones have often wrought in taxonomic work. He remarks "It cannot then be a matter of indifference to ecology or to plant-geography, for instance, whether the prostrate 'isoreagent,' say of *Atriplex litorale*, is a habitat modification, or a hereditary habitat type." In a recent paper (57, p. 19) he gives an interesting example (for *Succisa pratensis*) "wie die Modifikation die erbliche Variation deckt. Gewisse der Individuen sind *erbliche Zwerge*, andere sind nur *modifikativ*, auf Grund der extremen äusseren Verhältnisse zu Zwergen geworden." The junior author (3) has given a number of illustrations of epharmonic response and its bearing on taxonomy, and many others are to be seen in certain of the papers cited for the senior author. Here a few striking illustrations may be cited.

In the *Manual* (10, p. 500) two "varieties" are given under *Rubus cissoides*—*pauperatus* and *subpauperatus*. The first is an epharmone of exposed situations with the leaves much reduced. In this condition it is rarely, if ever, found in flower. But plants are to be found showing both the *pauperatus* and the "normal" form. *R. subpauperatus* is a distinct jordanon resembling *R. cissoides* only in a general way, and flowering freely in the open. This species is only in part the var. *subpauperatus* of Cheeseman.

The var. *minor* of *Lepidium tenuicaule*—Cheeseman (10, p. 175)—we have shown (26, p. 56) to be an epharmone. There are a number of alleged varieties calling for investigation, e.g. *Atriplex Buchanani* var. *tenuicaulis*, *Geniostoma ligustrifolium* var. *crassum*, *Hebe speciosa* var. *brevifolia*, *Coprosma rhamnoides* var. *vera* and var. *divaricata*. *Helichrysum depressum* is a depressed, dead-looking bushy shrub of river beds in South Island. In one locality of the Eastern Botanical District it is found as a perfectly prostrate plant, closely hugging the shingle. A close examination of the area by the junior author failed to find evidence that this prostrate form was an epharmone, and in an apparently precisely similar locality, not many miles distant, plants only of the "normal" form were found. These field observations need supplementing with cultural tests. *Alectryon excelsum* is well known on account of the dehiscent fruits disclosing brilliant scarlet arils. Observations over five seasons

at Feilding show that the vast majority of the fruits in that locality are indehiscent. Germination occurs freely when the fruits have lain for a long time on the ground and the cover begins to rot off. An examination of the aril shows it to be much reduced in size. Whether we are dealing with a non-dehiscent jordanon or what might be called a climatic epharmone cannot at present be said. Certain field observations in other localities suggest that the amount of dehiscence or non-dehiscence may differ from place to place, and from season to season, so that the phenomenon may be due to some physiological disturbance.

Nannfeldt (49, p. 413) has adopted Colenso's name *Centella uniflora* for the New Zealand forms of *Centella* hitherto referred to *C. asiatica*. His reasons seem to us perfectly cogent, but a thorough investigation of the New Zealand forms remains to be made. It is certain that epharmony plays a considerable part in producing the forms met with—see, e.g., our remarks (27, p. 62).

One jordanon of the nearly leafless *Carmichaelia subulata* spreads by underground stems that send up erect shoots at rather long intervals, so that what looks like a colony of separate plants is often a single individual. Growing on the exposed sea coast in grassland this form becomes much dwarfed, the shoots are sent up at short intervals and a loose cushion results, so that one unacquainted with the structure of the inland epharmone might consider that two distinct jordanons were in evidence—an error made by the senior author through faulty field observations.

Very suggestive is the fact that a jordanon in one species may be paralleled by an epharmone in another, or even in its own species. Thus there is a jordanon—var. *prostrata*—of *Hebe buxifolia* that rather closely hugs the ground. In the allied species *H. laevis* there may be found on the slopes of hollows where snow lies long a prostrate epharmone, which grows erect when transplanted into a garden; so too the erect *Hebe elliptica* has a prostrate epharmone.

A case of some taxonomic interest is that of *Schizeilema Allanii*. This was first collected by the junior author under subalpine scrub on a peak of the Ruahine Mountains. The scrub covered the summit of the mountain, and the *Schizeilema* was constant in form throughout. Cheeseman (10, p. 651) unhesitatingly described the plant as a new species. Later the junior author collected in several places on higher parts of the range, amongst subalpine grassland, a *Schizeilema* of more compact habit, but apparently structurally equivalent to the scrub plant. Also plants from the scrub grown in the garden have become much more compact in habit. Thus it would appear that the two forms belong to the same jordanon, but the type specimens belong to an epharmone of so distinctly different appearance from the later gatherings that seen merely as herbarium specimens the two would be considered specifically distinct. Indeed, it is by no means certain that both are not epharmones of *S. hydrocotyloides*.

A whole group that needs close study in the field and garden is that of the numerous large-leaved forms of the northern coastal islands—e.g. in *Macropiper*, *Nothopanax*, *Rhabdothamnus*, *Suttonia*, etc. Some of these have received varietal names, but in no case has a thorough examination of the possibilities been made—i.e. whether the forms are epharmones or jordanons, or in some cases possibly hybrids.

Our usage of the terms epharmone and epharmony does not correspond with the original signification of Vesque, as cited by Warming (58, p. 5), and waives the question of the “fixing” of epharmones in the course of time. It should be noted also that the criteria of an epharmone correspond with the “adaptative Merkmale” and not the “epharmonische Merkmale” of Diels (35, p. 137). It seems to us better to leave the term *modification* as a general physiological one, applicable to laboratory-made changes of form as well as to those of wild nature.

(e) *The Hybrids.*

Elsewhere (25, 27) we have already drawn attention to the importance of hybrids in connection with taxonomic problems, but a summary treatment is here demanded. The prevalence of wild hybrids in New Zealand needs emphasis. During the last decade a fair amount of attention has been given to the field study of wild hybrids, and although the Pteridophyta and Gymnospermae have as yet hardly been examined, well over 200 hybrids are known among the Angiospermae. To illustrate their prevalence we reproduce a table we have already published (27, p. 623) for the monocotyledons and dicotyledons. All genera containing 14 or more species are known to show inter-specific hybridism, if the strongest possible field evidence is accepted as decisive.

Classes of genera	Number of genera	Number possessing hybrids	Percentage possessing hybrids
Genera with 2-5 species	125	42	34
Genera with 6-10 species	33	17	52
Genera with 11-20 species	15	13	87
Genera with over 20 species	16	16	100

In addition much hybridism is known to occur among the jordanons of many compound species, but little exact work has been done among these. Very clearly to be realised is the fact that amongst hybridising species there occur in the majority of cases, not a few but a multitude of forms producing a motley “swarm.” From such swarms specimen after specimen may be chosen which on the herbarium plan could easily be considered as “distinct enough” to be treated as separate species. Of these swarms we have said (27, p. 623), “A hybrid swarm is a totally different biological group from that of a species. In the latter case there can be a ‘type,’ in the former a ‘type’ is impossible. Further, species deal with definite, static groups, but hybrid swarms

with indefinite dynamic groups, for the hybrids of to-day are being replaced before our eyes by other forms."

Though at least 45 almost certain cases of hybrids masquerading as species could be adduced from the *Manual* (10) we can have space for only one or two examples. Wherever *Myrtus bullata* and *M. obcordata* occur together a most diverse swarm of hybrids may be found. This was fully gone into by the senior author (22, p. 179), and there is not the slightest doubt that *M. Ralphii*, founded by Hooker in 1853 on a few specimens sent from Wellington, is merely one of the hybrid forms, rather closer to *bullata* than to *obcordata*. Yet Cheeseman (10, p. 597) accepts the species as valid since, he says, "I have been acquainted for 50 years with a locality for *M. Ralphii* in which, to the best of my belief, there are no specimens of *M. obcordata* within at least 20 miles, and none of *M. bullata* within 5 miles." This fairly sweeping statement postulates almost inconceivably intensive field work nor is it likely that the vegetation was even semi-virgin. Moreover, though he refers to the large number of the so-called hybrids "which give a certain amount of support to this [the hybrid] view" he does not deal with these in his Flora—his diagnosis of *M. Ralphii* referring to but a small portion of the swarm. That is to say hundreds of forms are simply ignored. The field evidence is indeed so overwhelming that we can see no force in Cheeseman's argument; nor can we see any reason for denying the power of a hybrid form to spread beyond the place of its origin to one where the parents do not occur. A much discussed case is that of the coastal forms of *Senecio* found along the western coast of the North-western Botanical District. Specimens thence have been variously referred to *S. rotundifolius* and *S. elaeagnifolius*. Cheeseman (10, p. 1026) makes the var. *ambiguus* of *S. rotundifolius* for some of these forms, remarking that it, "recedes from the type in the direction of *S. elaeagnifolius*, but in my opinion is best placed under *S. rotundifolius*...on the other hand, Petrie (*Trans. N.Z. Inst.* XLVI (1914) 30) 'refers without hesitation' the Cape Foulwind plant to *S. elaeagnifolius*. Cockayne [*Trans. N.Z. Inst.* 50 (1918) 184—citation in *Manual* incorrect] considers that the West Wanganui form is neither typical *S. rotundifolius* nor *S. elaeagnifolius*, but may be a variety of either." In the paper just cited the senior author said, "It seems clear that the taxonomic position of the West Wanganui inlet plant is quite uncertain." An examination of the forms in Petrie's herbarium, seen also by Cheeseman, shows that the two species in dispute are both present, along with hybrids between them.

No two species better show the insignia of jordanic distinction than *Wintera axillaris* and *W. colorata*. When growing apart from each other the two species faithfully reproduce their distinctive characters from seed. When they meet, however, they hybridise, and since they have overlapping altitudinal distributions, *W. colorata* ascending much higher, epharmony also comes into play. Petrie (50, p. 292), speaking of a certain forested ridge on Mount Hector (Ruahine-Cook Botanical District), says, "I was greatly interested in the

remarkable leaf-variation shown by *Drimys axillaris* at increasing elevations on this ridge." At the lower levels the leaves were "typical." "At increasing heights the leaves became progressively longer, narrower, and more acute, while the colour of the upper surface grew more and more decidedly red, and that of the under surface more and more decidedly a creamy yellow. At the highest levels at which it was observed the foliage had assumed a form barely distinguishable as regards the coloration of both leaf surfaces from the species known as *Drimys colorata*, so common on the edges of bush land in the lower parts of Otago and Southland, differing only in the longer, narrower, and more pointed leaves and the flat, even margins. Before seeing the series of forms growing on this ridge I was a firm believer in the specific distinctions of *Drimys colorata*, but the instructive series of leaf-variations here observed has considerably shaken my confidence in this opinion." We have studied the matter on this and other ridges, and find that there is often a belt where *W. axillaris* is pure, or largely predominant, that there succeeds a belt where both species occur, and that the diversity referred to by Petrie is due to hybridisation. There succeeds a belt in which *W. colorata* alone occurs and shows only such diversity as can be attributed to environmental influence. Cultivated in gardens the two species remain perfectly distinct. It may well be that the Otago and Southland jordanon of *W. colorata* is distinct from the northern one, but we are certain that *W. colorata* and *W. axillaris* are not epharmones of one and the same species.

Although polymorphic swarms of hybrids are what one usually meets with in the field, other cases occur. \times *Rubus Barkeri* is a plant now widespread in gardens, having been distributed by rooted cuttings. Only a single plant was found in the wild state, but a study of the plant leaves hardly a doubt that it has the parentage *R. australis* or *R. schmidelioides* var. *coloratus* \times *parvus*. Recently Dr McKay of Greymouth has discovered another wild hybrid plant of closely similar characters to \times *R. Barkeri*. Moreover, the junior author has been successful in raising artificial hybrids between *R. parvus* and *R. schmidelioides* that lend much support to the theory of the hybrid origin of *R. Barkeri*. Cheeseman (10, p. 501) refers to forms of *R. parvus* with paniculate inflorescences, and others with 3-foliate leaves are known. These forms, also, are probably of hybrid origin.

A good example of diversity due to hybridism is that of *Celmisia incana*. This is a compound species, of which one jordanon is extremely abundant on Mount Hauhungatahi (Volcanic Plateau Botanical District), forming large mats often several metres in extent. So far as the junior author's rather close examination revealed the species is perfectly constant all over the subalpine belt of the mountain. On the Ruahine Mountains (Ruahine-Cook Botanical District) there is great diversity, since there also occurs another species, generally referred to *C. discolor*, producing hybrid swarms with *C. incana*, and so too in various localities in South Island.

The results of collecting on the lines we have indicated, as against random gatherings, is illustrated by an excellent piece of work accomplished by Messrs J. Scott Thomson and G. Simpson on Rough Peaks (South Otago Botanical District, near its junction with the Fiord Botanical District). Full examination showed that there grew on the unstable debris slopes of those mountains a *Ranunculus*, which in the very many individuals studied was constant in form, and of which juvenile plants also showed no diversity. This jordanon when compared with other species proved to be undescribed, and is so markedly different from all others as to justify us in treating it as a "new" species—*Ranunculus Scott-Thomsonii*. On the same mountains grows *R. Buchanani*, possibly a jordanon of the compound species distinct from any other. This is a rock-plant that does not stray on to the debris slopes, but hybridises with the debris-slope plant at the margins, and produces a swarm of diverse progeny. Had the gatherings been made at haphazard no such useful information would have come to light. Contrary cases are those of *R. Mathewsii* and *R. Baughani* from the Fiord Botanical District, based in each case on a very few indiscriminately gathered scraps, and the former later proving to be founded on hybrid material, while the latter is most likely one of a hybrid swarm.

An important point that can only be elucidated by proper field methods is the occurrence of hybrid forms simulating jordanons—parallel to the simulation of jordanons by epharmones. *Coriaria lurida* occurs in two distinct jordanons on Mount Egmont. These hybridise together, and the larger jordanon also freely hybridises with the jordanon of *C. sarmentosa* occurring on the mountain. There is produced a completely intergrading series of forms linking up the three jordanons. An examination of a *Coriaria* swarm occurring near the Royal Peaks, made by Messrs Simpson and Thomson, showed a like diverse progeny between two jordanons of *C. sarmentosa* and *C. lurida* distinct from those occurring on Mount Egmont. Now the mid-forms of this series, seen as herbarium specimens, are closely similar to the larger-leaved jordanon of Mount Egmont, and would be placed along with it by a herbarium botanist ignorant of the field information available. The same collectors, while examining a swarm produced by *Aristotelia fruticosa* \times *serrata*, found a remarkable form with almost the leaf size of *serrata*, but quite lacking the distinct teeth possessed by both parents. While this form requires experimental study, a hybrid origin is strongly suggested by the field evidence. Had, however, this form alone been collected—as might easily have been the case with such a striking form by a collector whose thoughts were merely on something "new"—it might easily have been granted specific rank by a botanist who did not know the full field data as to its occurrence. This actually happened in the case of one form of the swarm, Hooker basing his *Aristotelia Colensoi* on non-flowering scraps from one individual which must have died long ago, so that the "species" is now non-existent.

Hybridism among the ferns has received little attention, but would provide a fertile field for investigation. Especially rich in hybrid forms is the group centering round *Asplenium bulbiferum*. This compound species is easily recognised in its so-called "typical" bulbiferous state (not the commonest form). Cheeseman (10, p. 50) recognises two varieties—var. *laxum* and var. *tripinnatum*—remarking, "when the bulbils are not developed and the frond is more slender, with narrower and more deeply divided pinnules, so that the sori are often almost marginal, the plant becomes var. *laxum*. This runs into several small states not clearly separable, one of which is the *A. triste* of Raoul, and another Colenso's *A. gracillimum*. Var. *tripinnatum* has still narrower pinnules, deeply cut into narrow linear segments, and the sori are quite marginal. It approaches very close to some states of *A. flaccidum*, but the frond is broader and more decompose, and the texture is thinner. In addition to the above varieties there are a large number of puzzling forms, which apparently connect the species with *A. falcatum*, *A. lucidum* var. *Lyallii*, *A. scleropium*, *A. Hookerianum*, *A. Richardi* and *A. flaccidum* [*A. obtusatum* and *A. Colensoi* might have been added]. In Stewart Island, passage forms into *A. scleropium* and *A. flaccidum* are particularly abundant, and it is often difficult to decide to which species they should be referred. It would occupy many pages to characterize these, and I doubt whether it is possible to define them in language sufficiently precise to enable them to be recognized with certainty." In other words the herbarium method confesses itself bankrupt. There remains to be attempted an analysis on natural lines, seeking field and cultural evidence as to which forms are jordanons, and which are hybrids, bearing also in mind the likelihood of epharmonic change. This task we think by no means an impossible one. Proper field observations of themselves give much evidence for distinguishing jordanons. Some of the species concerned are of widespread, others of local distribution, and comparative studies of a number of localities would cast much light on the situation. But the work must be done in the light of new field observations and not from ancient herbarium material and memory.

As examples of a moderately full preliminary analysis of a hybrid swarm, we may refer to the paper by the junior author (1, p. 310) on *Coprosma propinqua* × *robusta*, and that by the junior author in collaboration with Thomson and Simpson (4, p. 375) on *Hebe elliptica* × *salicifolia* var. *communis*.

There remains to give a brief résumé of the methods we have adopted in naming hybrid swarms. Further references to the matter will be found in our joint papers (25, p. 44, and 27, p. 623). For the hybrid swarm, imitating a certain horticultural practice, we construct a name by combining in an abbreviated form and with a suitably modified ending the names of the parent species. Thus *Danthonia pilosa* produces polymorphic swarms of hybrids with *D. semiannularis*. Our unpublished name—× *D. semipilosa*—will apply to all hybrid forms to be met with, no matter what jordanons of the two compound parental

species (and there are several such, not yet worked out) are concerned. The example given also illustrates the point that where one of the parental names is short it is preferably used in its entirety, and that where euphony demands the alphabetical order is to be departed from. Where a named jordanon is concerned the varietal name may be incorporated in the telescoped hybrid name, e.g. \times *Poa ansetipusilla* for the swarm arising from *P. anceps* \times *pusilla* var. *seticulmis*. Some ingenuity is of course often required to keep the name reasonably short, and not of greater absurdity than average specific name, while providing for one of its valuable features—the revealing to the reader acquainted with the names of New Zealand species the exact parentage involved.

For a number of New Zealand hybrid swarms a specific or varietal name has been given to a small group within the swarm, usually that of the series coming about midway between the parents. Thus \times *Hebe divergens* (\times *Veronica divergens* Cheesem.) refers to certain hybrid forms in the swarm \times *Hebe ellipsala* (*H. elliptica* \times *salicifolia*), the jordanons concerned being in this case unnamed. Such names we retain when they seem to serve a useful purpose, but we are strongly against widening the conception of such names to include the whole swarm, nor indeed have we any justification for doing so. Far better abandon altogether such false “species” than risk helping to perpetuate an error.

Art. 34 of the *International Rules of Botanical Nomenclature* states, “when there is reason to distinguish the different forms of a hybrid the subdivisions are classed under the hybrids like the subdivisions of species under a species. Examples: \times *Mentha villosa* β *Lamarckii* (\times *M. longifolia* \times *rotundifolia*).” Realising as we do from field studies that in so many hybrid swarms literally hundreds, perhaps thousands, of forms can be picked out by the trained eye, such giving of subordinate names would carry us to inordinate lengths. On the other hand the method suggested in Art. 34 for indicating “preponderance of the characters of one or other parent,” by use of the signs $>$ and $<$, and the neater method, supported by Diels (35, p. 176), of using such terms as “media” and “per” seems hardly to go far enough. Where, then, in analysing a hybrid group for special purposes it is desired to form minor groups we adopt a “formula treatment”—see, e.g., the junior author’s paper (2, p. 288). For the swarm \times *Melicope tersimplex* (*M. simplex* \times *ternata*), the formula reads T5, T4, T3, T2, T1, TS, S1, S2, S3, S4, S5. T5, T4 represent the “perternata,” S4, S5 the “persimplex,” and TS the “media” forms (these latter also roughly corresponding to \times *M. Mantellii*, which was described as a species). T2, T1, and S2, S1 approach TS from the *ternata* and the *simplex* side respectively, and may be considered as “sub” forms. But a form may be “per” as regards one parent, and “sub” as regards another, while the formula represents an arrangement based on a balancing of the various characteristics shown by the forms found. This treatment seems sufficient for general purposes, and not so detailed as to defeat its own ends.

In floras the general name, with some reference to the degree of diversity existing, may be all that space allows, but in a detailed analysis of a particular swarm and in monographic treatment of genera and species the formula will have its place.

For inter-generic hybrids similar telescoping of the generic names may be used with advantage. This has also already been done in horticultural practice, and is recommended by Diels (35, p. 104), who gives the example: *Odontoglossum* \times *Cochlioda* = \times *Odontioda*. *Helichrysum pauciflorum* was described by T. Kirk (44, p. 351) from material gathered by the senior author. The latter has long suspected that the plant was a hybrid. Recently Prof. Wall, after an examination of Petrie's herbarium, suggested that we should look into the question as to whether *Raoulia Gibbsii* were not the same species as *Helichrysum pauciflorum*. The senior author, after a study of the material in the herbarium came to the conclusion that the specimens concerned belonged to the swarm *Leucogenes grandiceps* \times *Raoulia bryoides*. Should this opinion be substantiated we would use the name \times *Leucoraoulia* for the swarm.

(f) *The Linneon.*

Reference has been made to the linneon *Olearia arborescens*. A further case or two will serve to summarise the various grades of individuals and groups that concern the taxonomist. Of *Craspedia uniflora* Cheeseman (10, p. 989) remarks, "The New Zealand species has the range of the genus [N.Z., Australia, Tasmania]...A most variable plant. The three varieties described above look very distinct in their extreme forms, but are connected with the ordinary state of the species by numerous intermediates." Now, what Cheeseman considered to be the "ordinary" state we do not know, nor how far all or any of the New Zealand forms are identical with those of Australia and Tasmania. But, this apart, to group all the New Zealand forms of *Craspedia* into one species is at once to create a linneon, made up of jordanons, hybrids and epharmones. Cheeseman gives no details of the distribution of the varieties he allows. The genus was published by G. Forster (39, p. 58), and one species named—*uniflora*—but without specific diagnosis, so that without examination of the type specimens we cannot guess what form or forms are included. It will suffice to indicate the groups field studies, still very far from complete, have revealed. There is, then: (1) A group of coastal forms—some of these are large leaved and come under "var." *robusta*, in the general sense in which that name is used. There are also smaller-leaved forms. One quite showy and very distinct coastal jordanon we propose to name *C. maritima*. (2) A group of tussock-grassland and open shrubland forms, including those often called by the "varietal" names *fibriata*, *viscosa* and *minor*, as well as some *robusta* forms. There are certainly several distinct jordanons included, and many hybrid forms. Until proper field study has been made the attaching of the above "varietal" names to their specimens by collectors is worse than futile, as it

implies a definite knowledge that is certainly not possessed. (3) A group of forms of damp places, streamsides both in the open and the forest, etc. Probably many of these are epharmones of the second group, but no research on them has yet been attempted. (4) The distinct jordanon, *C. alpina*, of unstable debris slopes. This hybridises with some of the tussock-grassland forms. The linneon thus contains several distinct jordanons deserving specific rank, probably several varietal jordanons, numerous hybrids, and an unknown but probably considerable number of epharmones. This group would certainly reward investigation on ecotype lines, but to us it appears that the analysis of the forms as to their status must first be fairly well worked out.

Finally a linneon may be discussed of which the study has advanced to a greater extent—*Hebe salicifolia*. The varieties accepted by Cheeseman (10, p. 790) are of different classes: (1) var. *stricta*, "the common variety in the North Island." There are a number of jordanons in North Island, and "var." *stricta* is at present but a name for the residue of unresolved jordanons, hybrids and epharmones. What the original var. *stricta* Banks et fol. ex Benth. may be is another matter. (2) var. *longiracemosa*. This is a jordanon, mainly if not solely, of the Egmont Wanganui Botanical District, though Cheeseman attaches to it herbarium specimens from the Waitakerei Range (South Auckland Botanical District). (3) var. *paludosa*. This is a very distinct jordanon of swamps of the North-western and Western Botanical District of South Island. Whether Cheeseman is correct in including with it a jordanon growing on Mount Egmont in subalpine scrub remains to be decided. The two are certainly very closely allied, though of markedly different habitat. (4) var. *Atkinsonii*. This is a compound variety already referred to as being retained under *salicifolia* only because one of its jordanons may prove to be the type of that species. (5) var. *Kirkii*. Field evidence makes it clear that \times *Hebe Kirkii* is a hybrid of the origin *H. leiophylla* \times *salicifolia* var. *communis*. Plants referred to \times *H. Kirkii* are the LS forms of the swarm \times *H. leiosala*.

Cheeseman places var. *communis* as a synonym of *H. salicifolia*, apparently regarding it as the type, although his general description obviously does not correspond with var. *communis* or any other jordanon, but is of a mixture of forms. Var. *communis* is a widely distributed South Island jordanon, and even if the type—very probably it is not—must retain according to our usage its varietal name. To speak of *Hebe salicifolia* in the usual loose way is thus to refer to a vast linneon; indeed its interspecific hybrids with *H. macroura*, *H. angustifolia* and other species often receive this all-inclusive and for most purposes quite useless bald naming.

8. PROBLEMS CONNECTED WITH DISTRIBUTION.

While anything like a full discussion of problems of distribution as revealed by field studies in New Zealand would lead us too far from the main purpose of this paper, a short reference seems demanded. The point we wish to stress

is that until the linneons forming so large a proportion of our flora, as given in the *Manual* (10), are much more fully analysed one cannot feel comfortable in drawing sweeping conclusions as to distribution within New Zealand itself. Still less are we in a satisfactory position as regards the many alleged "wides" of the flora. This is the more necessary to point out as Willis (see, e.g. 59, p. 56 *et seq.*) uses New Zealand data very largely as a basis for his far-reaching and much-discussed theory of "Age and Area."¹

That there are many unsolved problems as to the actual distribution of jordanons, for example, in New Zealand, both from the geographical standpoint and from the ecological will have become clear to those who have read thus far, and in conclusion a few more cases may be given to clinch the matter. It has only recently, for instance, become clear that as regards *Rubus australis* there are distinct jordanons of more or less restricted range, some perhaps confined to North Island, some to South Island. Indeed as regards several of the "best known" species, e.g. *Nothopanax arboreum*, *Carpodetus serratus*, *Veronica Lyallii*, *Meliccytus lanceolatus*, the jordanic distribution as between island and island is coming to the front. And as intensive work develops so the complexity of the matter becomes the more evident. The distribution of *Coprosma parviflora* was simply expressed so long as no attempt was made to analyse that linneon—"abundant throughout." But so soon as it became clear that *C. myrtillofolia* was distinct from *C. parviflora* proper it was realised how little we really know on the subject. The genus *Alseuosmia*, extending from North Cape to Westland, is one in which we are all at sea as to the status of the individual forms. Hybridism runs riot, epharmony undoubtedly plays a part, and the jordanons—whatever they may be—are probably, some or all, compound. while some at any rate are heteroblastic in development. The usual treatment in herbaria and floras is futile, and amounts merely to bringing together into groups specimens that more or less resemble one another. Cunningham (30, p. 209) established the genus and sorted his material into 8 "species." Hooker (42, p. 109) reduced these to 4, and his treatment has been followed by subsequent systematists, with or without the recognition of "varieties." Cheeseman (10, p. 881) says, "The species are exceedingly variable and difficult of discrimination." The genus would provide excellent material for any New Zealand botanist wishing to test the efficacy of the methods in this paper. He should, however, realise that this would be a matter of years not days and would prove a strenuous task: preconceived ideas would have to be abandoned. But until the analysis of this and other linneons is made they cannot serve for drawing conclusions as to "age and area" that will have more than speculative value.

So too our knowledge of *Poa caespitosa* and species after species is, from the standpoint of this paper, in its infancy. In fact, it is little exaggeration to declare that the commoner a species is the less is known about it! Would that

¹ We have in preparation a paper giving the views we have arrived at on this question.

the number of workers were commensurate with the number of pressing problems! And would that new workers, free from the thralldom of the dangerous herbarium artificial method, would come forth.

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THE PLANT COMMUNITIES OF TABLE MOUNTAIN: PRELIMINARY ACCOUNT

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(With Plates IX and X and one Figure in the Text.)

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INTRODUCTION.

The present is a preliminary account of the general features of the plant covering of Table Mountain, and of the relationships of the communities, especially in regard to succession. This account is of the nature of an introduction to more detailed studies of the problems arising in connection with the vegetation on this mountain and in the sclerophyll type in South Africa in general. Work on some of these problems is being undertaken at present.

POSITION.

Table Mountain, which rises to a height of 3586 ft. (1093.1 m.), lies about 33.57 S. Lat. and 18.25 E. Long. It forms the northern end and highest point of the ridge that constitutes the Cape Peninsula. The mountain is well named as it is a flat-topped mass that rises very steeply from the sea on the west and

north, and from the flat, low-lying land that joins the peninsula to the mainland on the east. The summit of the mountain is only about three miles from the seashore of Table Bay. The summit lies on a fairly level plateau, extending two miles in the east and west direction, which drops very steeply in cliffs 500–1500 ft. (150–450 m.) in height on the north, west and east sides. To the south there is a more gradual fall to a lower plateau, with an altitude of 2000–2500 ft. (600–700 m.) which extends for some miles, though cut into by stream channels. This lower plateau is again bounded by cliffs but of rather less extent. Below the cliffs the ground is less broken but often of considerable angle of slope.

GEOLOGY¹.

The physical features of the mountain are closely related to the geological structure. The mountain is formed by a mass of horizontal sandstone, Table Mountain Sandstone, which lies unconformably on older rocks. These older rocks consist of a coarse-grained granite that has been intruded into a series of rather contorted and highly tilted slates, Malmesbury Slates. The plateau and cliffs are composed of the Table Mountain Sandstone, the less broken lower slopes of the older, so-called Pre-Cape rocks. The sandstone is a hard quartzitic grit.

SOILS.

The soils vary very considerably with the character of the underlying rocks, though all are of the siliceous type. The Malmesbury Slates and granite give rise to a fine-grained rather claylike soil which is often of considerable depth. The granite soils contain a large admixture of gravel and are easily weathered; in places the drainage channels have cut “dongas” that may be 12–20 ft. in depth, with very steep sides. Practically all the soils on the lower slopes, and especially those near the drainage channels, have a considerable mixture of sandstone, either as blocks or more broken down, brought down from the cliffs above. Most of the soils are very full of stones. Every variety of soils can be found on these lower slopes from a stiff clay to an almost pure sand. Most agree, however, in being relatively deep. Indeed the deep penetration of roots is quite a notable feature; frequent examples can be seen of shrub roots at a depth of 10–15 ft. from the surface. The soils derived from the sandstone are coarse grained and generally shallow, though even here roots penetrate to considerable depths along cracks and joints in the underlying rocks. The amount of humus in the soils is very variable; it is small in most of the granite and slate soils. On the sandstone, and especially at the higher altitudes and where moisture is present, a high percentage of humus is present. Some of the more detailed features of the soils are mentioned later in connection with the descriptions of the vegetation.

¹ Cf. **Rogers and du Toit**, 1909.

CLIMATE.

The climate is a warm temperate one with the major part of the rainfall in the winter months and a relatively dry summer. Owing to the proximity to the sea and the frequent moist cooling winds in summer, the climate is equable and somewhat oceanic in type. The extremes of temperature are not great; the mean monthly temperature varies between 54° F. (12.2° C.) and 69° F. (20.4° C.) with a mean maximum of 101° F. (37.6° C.) and a mean minimum of 34° F. (1.1° C.)¹. Frost is unknown at sea level and even on the mountain the amount and severity of frosts are not great. Snow is of rare occurrence and, when it does fall, it melts and disappears very quickly. The

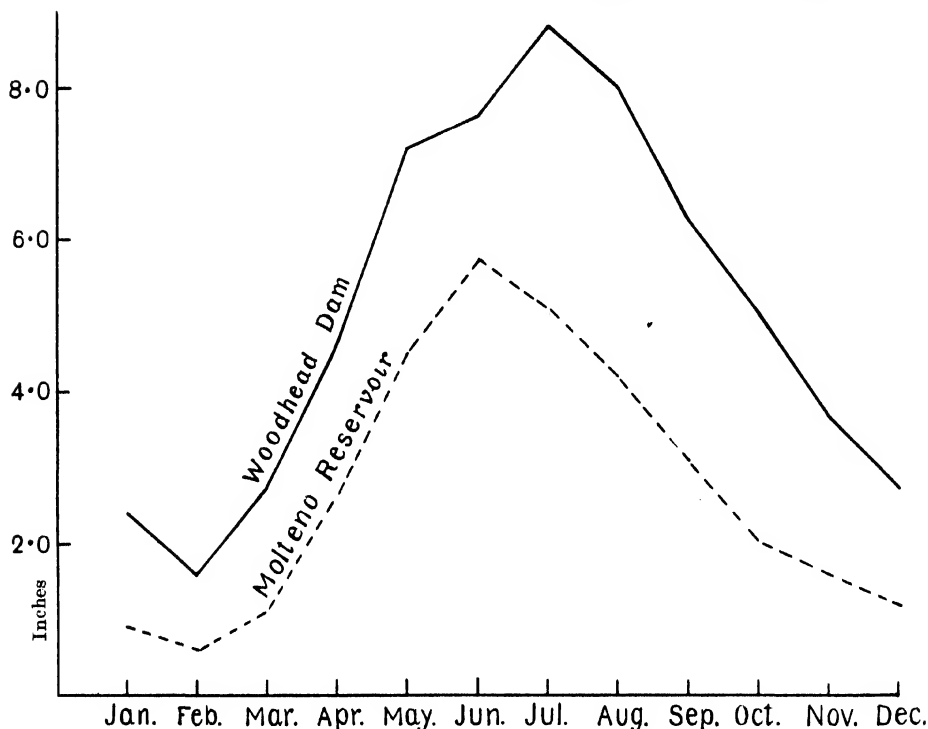


FIG. 1. Rainfall.

relative humidity is moderately high; the monthly means vary between 80–81 in winter and 67–69 in summer. During the day in summer the relative humidity may fall as low as 35. Even in summer dew is of common occurrence on the mountain.

Winds are frequent and often violent throughout the year. The prevailing winds are S. or S.E., though W. and N.W. winds are frequent in winter and to these is due the rainfall. Wind, and especially the S.E. wind, is a marked factor in the climate. The strength and prevalence are noticeable in the form

¹ Knox, 1911.

of many trees and larger plants¹. The cool S.E. winds in summer form a condensation cloud on the mountain, the so-called "Table Cloth," even when the atmosphere below is clear and relatively dry. This condensation cloud, which is especially frequent in summer, is a marked factor influencing the vegetation. Marloth² has shown that these mists result in a very considerable deposition of moisture on the plants while an ordinary rain gauge recorded no precipitation. Even though the figures given may be open to question in regard to absolute accuracy³, there can be no doubt on the general question that these frequent mists do provide a source of water that becomes available to the plants and that they very decidedly modify the climate. The difference in freshness of the vegetation, and in the amount of water in the mountain springs after a period of S.E. mists and in a year when these have been few, or absent, is obvious to the most casual observer.

RAINFALL.

The total rainfall recorded on different parts of the mountain shows a remarkable amount of variation for so small an area. The following figures taken from the published data of Stewart (1913) and of Cox (1922) will illustrate this feature. Stations on the north side of the mountain are:

Cape Town (Fire Station)	25.64 in. (651.2 mm.)
Moltene Reservoir (500 ft.)	33.16 in. (842.2 mm.)
Platteklip (750 ft.)	45.12 in. (1146.0 mm.)

While on the west side the figures are:

Camps Bay	24.25 in. (615.9 mm.)
Sea Point	24.45 in. (611.0 mm.)

Much higher figures are recorded on the eastern side:

Kenilworth	47.09 in. (1196.0 mm.)
Wynberg	42.24 in. (1072.8 mm.)
Newlands	52.20 in. (1325.8 mm.)

On the mountain itself the following are records for a 19-year period:

McLear's Beacon (3586 ft.)	89.30 in. (2269.2 mm.)
Waai Kopje (3100 ft.)	69.19 in. (1757.4 mm.)
Disa Head (2500 ft.)	36.55 in. (928.3 mm.)
Kasteel Poort (2483 ft.)	61.21 in. (1554.7 mm.)

These figures bring out clearly the very much larger amount of moisture in the upper portions and on the eastern slopes of the mountain. This increased moisture, which is the result of the increased precipitation, is accentuated by the increased humidity resulting from the frequent mists on the mountain top and the shelter from the sun on the eastern slopes. The rainfall records, irrespective of the differences in total, all show the same character, namely a maximum precipitation in winter. The summer months, October to March, receive only about 25 per cent. or less of the total rainfall, and of this amount, a considerable percentage may be looked upon as non-effective, owing to the falls occurring as light showers or mist condensations that are very soon

¹ Marloth, 1908, etc.

² Marloth, 1904, 1905.

³ Stewart, 1904.

evaporated. The following tables give some details of the rainfall at stations on the mountain. They are based on data supplied to me through the kindness of the City Engineer of the City of Cape Town, to whom I take this opportunity of expressing my thanks. The stations are the Woodhead Dam on the lower plateau of the mountain, the Molteno Reservoir in Cape Town on the lower northern slopes, and at Kloof Nek, the junction between the mountain itself and the Lion's Head. Among other features the much greater annual variation at the lower station is worthy of note.

Table I. *Rainfall at Woodhead Dam. 2413 ft. (735·4 m.).*

		Average annual rainfall (32 years)		64·61 in. (1641·09 mm.)			
		Maximum		,,		87·53 in. (2283·2 mm.)	
		Minimum		,,		46·92 in. (1191·76 mm.)	
						No. of records	
						above	below
						10 in.	1 in.
						(254 mm.)	(25·4 mm.)
Month	Average		Maximum		Minimum		
	in.	mm.	in.	mm.	in.	mm.	
Jan.	2·44	61·98	9·97	253·24	0·24	6·10	0 5
Feb.	1·63	41·40	4·18	106·17	0·13	3·30	0 10
Mar.	2·78	70·61	6·26	159·0	0·29	7·37	0 3
Apr.	4·69	119·13	11·39	289·31	1·20	30·48	1 0
May	7·27	184·66	13·53	343·66	1·35	34·29	6 0
June	7·63	193·8	22·52	572·01	3·29	83·57	14 0
July	8·86	225·04	16·51	419·35	2·89	73·41	13 0
Aug.	8·02	203·70	19·04	483·62	1·28	32·51	8 0
Sept.	6·36	161·54	12·56	319·02	1·90	48·26	4 0
Oct.	5·02	127·51	11·87	301·50	2·19	55·63	1 0
Nov.	3·67	93·22	9·36	237·74	1·00	25·4	0 0
Dec.	2·72	69·60	10·34	262·64	0·29	7·37	1 6

Table II. *Rainfall at Molteno Reservoir, Cape Town.*

Average annual rainfall (38 years) 33·09 in. (840·49 mm.)							No. of records <div>above below</div> <div>10 in. 1 in.</div> <div>(254 mm.)(25·4mm.)</div>		
Maximum		,,		,,		47·17 in. (1198·11 mm.)			
Minimum		,,		,,		21·72 in. (551·08 mm.)			
Month	Average		Maximum		Minimum				
	in.	mm.	in.	mm.	in.	mm.			
Jan.	0·96	24·38	6·87	174·50	Nil.		0	30	
Feb.	0·64	16·26	2·42	61·47	Nil.		0	29	
Mar.	1·11	28·19	3·25	82·55	0·01	0·25	0	20	
Apr.	2·60	66·04	6·88	174·75	0·17	4·32	0	5	
May	4·54	115·32	8·78	223·01	0·60	15·24	0	1	
June	5·76	146·30	16·20	411·48	1·00	25·4	3	0	
July	5·17	131·32	11·12	282·45	1·27	32·26	2	0	
Aug.	4·26	108·20	11·57	293·88	0·65	16·51	2	2	
Sept.	3·10	78·74	7·37	187·20	1·16	29·46	0	0	
Oct.	2·07	52·58	5·14	130·56	0·39	9·91	0	6	
Nov.	1·60	40·64	6·04	153·42	0·15	3·81	0	13	
Dec.	1·27	32·26	5·62	142·75	0·02	0·51	0	21	

Table III. *Rainfall at Kloof Nek, Table Mountain.*

Month	1923		1924		1925		1926	
	in.	mm.	in.	mm.	in.	mm.	in.	mm.
Jan.	—	—	0.55	13.97	0.93	23.62	0.38	9.65
Feb.	—	—	0.18	4.57	0.24	6.10	1.35	34.29
Mar.	—	—	1.54	39.12	0.01	0.25	0.22	5.59
Apr.	—	—	1.29	32.77	0.83	21.08	1.84	46.74
May	6.95	176.53	2.51	63.75	2.04	51.82	5.23	132.84
June	8.12	206.25	5.20	132.08	8.10	205.74	1.83	46.48
July	5.13	130.30	2.09	53.09	6.17	156.72	4.78	121.41
Aug.	4.01	101.85	4.62	117.35	2.95	74.93	—	—
Sept.	3.71	94.23	2.91	73.91	2.38	60.45	—	—
Oct.	1.54	39.12	2.10	53.34	3.77	95.76	—	—
Nov	6.14	155.96	2.67	67.82	2.81	72.22	—	—
Dec.	0.25	6.35	Nil.	—	0.62	15.75	—	—
Total	—	—	25.66	651.76	30.85	783.59	—	—

VEGETATION.

PREVIOUS WORK.

The vegetation of Table Mountain is undoubtedly the best known and most studied in the southern part of Africa. The general features of the vegetation have been frequently described, and the similarities and differences that appear in a comparison with other regions of similar climate have often been mentioned¹. Most of the earlier accounts are either of a very generalised kind or are primarily floristic. Two features have called forth general comment, namely, the great diversity and richness of the flora in a very small area² and the great uniformity in the life forms and also leaf characters. From sea level to the mountain summit the uniformity in the aspect of the vegetation is a striking phenomenon³.

Of work of a definitely ecological nature, the account given by Marloth in "Das Kapland" is by far the most complete and the most important⁴. In this work Marloth gives a full descriptive account of the vegetation of Table Mountain, but he does not pay very much attention to the phenomena of succession and development which are emphasised at present. While many of the descriptive parts that follow are of necessity a repetition of Marloth's very accurate observations, the different point of view adopted and the changes brought forward in the scheme of classification of the plant communities are such that the repetition is warranted. Marloth makes a first division of the vegetation in accordance with the physiographic and geological features; the lower slopes, and the plateau and cliffs. In the former, lower slopes, he distinguishes two types of vegetation: (1) "Macchia," composed of large bushes or small trees which frequently have flat leaves, and (2) "Hügelheide," composed of much smaller shrubs or bushes with a prevailing ericoid habit. This is treated as a subformation of the Macchia but distinct from that. He describes,

¹ References to older work in **Bolus**, 1905; **Marloth**, 1908.

² **Bolus** and **Wolley Dod**, 1903.

³ Cf. **Engler**, 1903; **Diels**, 1897.

⁴ **Marloth**, 1908.

however, examples where "Hügelheide" develops naturally into *Macchia*. In his second division, "Bergregion," he has three types: (1) "Felsenheide," the communities of the sandstone cliffs and of the horizontal exposed sandstone of the summit; (2) "Bergheide," or communities of the plateau; and (3) Bog and streamside communities. Marloth also describes the forests which occur in the more sheltered kloofs. These he regards as belonging to a quite different vegetation type from the other communities.

Some contributions to the ecology of Table Mountain have been made by Bews¹ who has indicated some successional features. His accounts are rather in the nature of notes than detailed studies. In his earlier work he distinguished three climax communities; "Fellfield," an essentially open community composed of lithophytes and chomophytes; Heath; and "*Macchia*." These correspond very closely to Marloth's "Felsenheide," "Hügelheide," and "*Macchia*." The Bergheide is not regarded as a unit, as Bews points out it is composed of hygrophilous and xerophilous constituents. The forest is treated as a separate unit. In his later work² he recognises three general successions, lithosere, hydrosere and psammosere. He further admits that the heath is frequently seral to *Macchia* and that *Macchia* passes into forest. Of other work, mention must be made of the account of regeneration of the vegetation after fire that has been done by Michell³ on Signal Hill. The early stages of regrowth on a soil derived from Malmesbury Slates are described and some features of the succession are investigated.

GENERAL.

As has been mentioned, on a first glance one of the most striking features of the plant covering of Table Mountain is the uniformity of growth form; except in the deeper and more sheltered ravines there is a general absence of trees. The prevailing type is a shrub or bush with evergreen, xerophytic leaves which are usually of a small size. This uniformity of growth form is, however, accompanied by a great diversity of species. Not only is the total flora a large one⁴, but practically all the communities have a large and diverse population. In very few cases can one, or even a group of species be said to dominate in the sense of determining the growth and development of the whole community. These communities, with their large populations, give a first impression of extreme diversity and of apparent lack of direct correlation with the habitat factors. Further study shows that this lack of correlation is due to interference with the vegetation and to destruction of the communities of plants and alteration of the normal development. This interference has been very considerable in its extent so that there are very few, if any, portions of the mountain that can be regarded as in their primaeval state. The interference has been caused by the felling of timber or firewood, grazing, planting, and burning.

¹ Bews, 1916.

² Bews, 1918, 1925.

³ Michell, 1922.

⁴ Cf. Bolus and Wolley Dod, 1903.



FIG. 1. Map of Table Mountain and Cape Town. Scale 1 in. to 3 miles (c. 1 : 100,000). (Reduced from map published by *Cape Times*, Ltd.)



FIG. 2. Part of Table Mountain from Cape Town, showing general features. The darker vegetation at the base of the slopes is composed of introduced pines. The palest parts are those recently burnt.



FIG. 4. *Protea* bush on west side. *P. laurifolia*, *Metastasis*



FIG. 3. Summit of Table Mountain. Vegetation largely composed of

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Of these, the last, fire, has been very much the most extensive and far-reaching in its effects. How long the occurrence of veld fires has continued is difficult to say, but it seems certain that the practice of burning the bushes has continued since the advent of the European settlers in this country nearly 300 years ago, and it is probable that occasional fires occurred before that time^{1, 2}. At the present time, and for many years past, some portion of the mountain suffers in this way each season. The result of these continually recurring fires is that the existing vegetation is made up of a patchwork of communities representing stages, more or less advanced, in the regrowth after destruction. Thus, on apparently identical conditions of soil, exposure, etc., are found adjacent communities, composed of quite different plants, due to the different time intervals since the previous fire. In no case has a community been noted in which direct reproduction takes place after fire. The effects of burning are so widespread and obvious that the other interfering factors appear of very much less importance. Their action has been certainly much more local; some of the effects are considered later. As the result of tree planting and pasturing of stock, the native vegetation has almost wholly disappeared from the basal slopes on the north and east sides of the mountain.

For purposes of description two general types of vegetation are recognised, namely, what may be termed the sclerophyll type which is by far the most abundant and extensive, on the one hand, and, on the other, the forests which occur in ravines for the most part. This division is that made by Marloth³ and further his division of the sclerophyll vegetation into that of the lower slopes and that of the cliffs and plateau is also followed here. A few notes on plantations and introduced plants are added. In this preliminary account no attempt is made to give complete lists of the populations of the communities. These are often so large that the complete lists would tend to bewilder rather than to enlighten. Instead, only the most abundant and most characteristic of the plants are mentioned. The attempt is made to give an idea of the general physiognomy and structure of the communities with a view to elucidating their relationships to one another and to their habitats. For this end use is made of the statistical methods devised by Raunkiaer both as regards life forms and leaf sizes⁴.

SCLEROPHYLL VEGETATION.

Lower Slopes.

Of the various sclerophyll communities of the lower slopes two stand out by reason of their greater complexity and less degree of xerophytism. These are the communities of large bushes among which the Proteaceae play the dominating rôle, and the open woodlands of the silver tree, *Leucadendron argenteum*. These communities are to be regarded as the climax types on these

¹ Cf. Marloth, 1908; Michell, 1922; Botha, 1924.

² Theal, 1882.

³ Marloth, 1908.

⁴ Smith, 1913; Fuller and Bakke, 1918.

slopes: the names "*Protea* bush," and "*Leucadendron argenteum* groves" employed in a previous account may be used for the sake of convenience¹.

Protea Bush. This is the more extensive and will be described first. While considerable variations in composition occur in different examples, there is a general uniformity in the structure of this type of community. The dominating plants, which form the uppermost stratum, are large bushes or even small trees with evergreen leaves of a hard texture. The leaves are of the sclerophyll type though often rather large: they are typically isobilateral and placed in the vertical position. The bushes are from 1 to 4 m. high. The most abundant plants are *Protea lepidocarpodendron*, on the northern and western sides, and *P. incompta* on the sheltered eastern slopes. The leaves of the former are much harder and thicker than those of the latter. Among other large shrubs of frequent occurrence are *P. grandiflora*, with large wax covered leaves, *Leucospermum conocarpum*, especially on sandstone talus, and less often *Protea mellifera*, on sand at low levels, and *P. speciosa* at higher altitudes.

These large bushes do not attain complete dominance. There are frequent gaps in the canopy which are occupied by smaller bushes.

The communities on the sheltered eastern slopes exhibit considerable differences from those on the exposed western or northern sides, and will be described first. These are dominated by *Protea incompta* and are certainly the less xerophytic. There is a very dense growth that is arranged in several layers: the large Proteaceous shrubs form the top layer; below these in stature but occupying alternating positions are smaller woody plants of which *Rhus tomentosa*, *R. lucida*, and *Passerina vulgaris* are the most abundant. *Widdringtonia cupressoides* is a not infrequent constituent here. Below these is a layer of undershrubs that often forms a very dense and almost impassable tangle. Among the most abundant are: *Felicia aethiopica*, *Stoebe alopecuroides*, *Pelargonium cucullatum*, with *Pteridium aquilinum*, *Aristea capitata* and a host of others in lesser quantity. The whole mass often becomes somewhat bound together by *Cassytha capensis*, *Fagelia bituminosa*, *Asparagus* and other scramblers and half scramblers. On the ground below the larger bushes are herbaceous plants among which are a number of true shade species such as *Crassula septas*, *Zantedeschia aethiopica*, *Cheilanthes multifida*, *Blechnum australe*, and *Haemanthus coccineus*, along with several species of *Oxalis* and other geophytes.

The community as it is developed on the western slopes is of a much more xerophytic type and has a less complex structure. The dominating shrub, *Protea lepidocarpodendron*, is a smaller plant, rarely exceeding 2.5-3 m. in height, and often less. The community is less distinctly layered: below and between the larger bushes is a dense growth of shrubs with small ericoid leaves. *Metalasia muricata*, *Anthospermum aethiopicum*, *Stoebe fusca*, and various species of *Erica* (*E. baccans*, *E. petiveri*, *E. pluckenetii*, etc.) are the most abundant.

¹ Adamson, 1925.

The shelter loving species such as *Rhus tomentosa*, *Widdringtonia*, *Aristea*, and *Pteridium* are quite absent. This feature is still more marked in the lowest ground layer, where, on the western slopes, sciaphytes are wanting; the ground layer is occupied by grasses and Cyperaceous plants with *Oxalis variabilis*, *O. obtusa*, *O. bifida*, and some other plants. Along stream channels on the west side the community approaches very closely to that of the eastern side. Here there is a much greater luxuriance and shade plants, ferns and others, are found.

The floral composition of the communities on the two slopes is markedly different. For example, a list made on the east side contained 91 species of vascular plants while a corresponding sample on the west had 93. Of these only 28 species occurred in both, a percentage of 18 of the total flora. This very small percentage of community is perhaps a little misleading: as the similarities of the floras are much greater than the numbers would suggest. A comparison of the lists of the two samples reveals the fact that while the species are different the genera are almost identical. In this exceedingly rich flora the presence of allied species in habitats of slightly different nature is of common occurrence and one that seriously complicates arithmetical statistics.

There can be no doubt that the two types are very closely allied ecologically. This is brought out by the similarities in the life-form spectra:

Total	M.	N.	Ch.	H.	G.	T.	E. ¹	
91	4	42	11	16	20	5	1	East side
93	4	37	14	18	19	7	—	West side

[Note. The single epiphyte is a parasite, *Cassytha* (cf. **Adamson** and **Osborn**, 1922).]

Taking the leaf size classes of the phanerophytes, the following percentages occur:

	Mic-meso.	Mic.	Nano.	Lepto.	Compound
East	4	22	28	32	16
West	4	12	26	50	8

The difference here expresses the increased xerophytism of the west side. When these figures are considered along with the similarities in structure and ecological relationships, which are discussed later, it appears to be justifiable to group the two together and to regard them both as climax communities (associations) of a single vegetation type (formation)². They are the resultants of the differing conditions on similar lines of development.

Other variations of this climax type of community are found. On sandstone talus, and especially where blocks of sandstone occur, *Leucospermum conocarpum* is the character plant. This plant has more the habit of a tree than *Protea*; it forms a single main stem. The individuals in a community are separated from one another. The associated plants are very similar to those of the *Protea* communities but owing to the lesser degree of cover are of a more xerophytic kind.

¹ In this, and all tables, the percentages are calculated to the nearest whole number.

² Cf. **Clements**, 1916.

On the shallower and more sandy soils *Protea grandiflora* is the dominant: this plant extends on to the lower levels of the sandstone proper.

Where conditions are suitable these *Protea* bush communities extend up to a height of 2300 ft. (700 m.).

Leucadendron argenteum Groves. These are the only tree communities in the sclerophyll regions. At the present time the distribution of the silver tree is very limited. It occurs on various soils on the lower slopes in rather isolated patches. The only parts where the tree covers any extent of ground are on the Lion's Head, at Kirstenbosch and Wynberg Hill, and on parts of the slopes of Orange Kloof. The tree is quite absent from the west slopes of the mountain proper, and never abundant on the northern side. Only in very sheltered spots does it occur above 1500 ft. (460 m.).

Leucadendron argenteum is exceptional, not only in having the tree habit, but also in possessing leaves covered with silky hairs. Hairy leaves are quite exceptional among the larger plants of these sclerophyll communities.

This tree forms open woodlands with no closure of the canopy and hence exerts a comparatively small degree of influence on the development of the associated plants. These are for the most part the same as those occurring in the *Protea* bush. This *Leucadendron* community forms another climax unit here, though what are its exact relationships to the previously described types is a question at present not solved but one that is being investigated. In the majority of cases the community appears to be stationary or even decreasing in extent, though there are examples where reproduction of the character plant is occurring quite readily, and all ages can be found associated together. One phenomenon may be mentioned in passing, namely, the frequent occurrence of dead silver trees. Isolated individuals of various ages die off, while those around appear quite normal; this and other features of the plant are under investigation.

Seral Communities. These bush or tree communities are the most complex and are regarded as climax communities, yet at the present time they are of limited extent and occupy a very small percentage of the total area of the lower slopes. A very much greater extent is occupied by simpler communities of small ericoid shrubs, of xerophytic monocotyledons, or others. These various communities are more xerophytic and occur for the most part on soils with less humus. All of them are regarded as stages in succession leading to the climax. Very few are examples of the primary successions; the vast majority are stages of regrowth following destruction by fire.

A fire attacking the climax *Protea* bush causes a destruction of the dominating shrubs. *Protea lepidocarpodendron*, *P. incompta*, *Erica* spp. and many others show no power of sprouting after burning and can only reproduce themselves from seed. On the other hand, *Protea grandiflora* regularly sprouts from the stool, while *Leucospermum conocarpum*, with its very thick development of cork, often survives a ground fire and continues growth. Trees that do this

assume an umbrella-shaped form owing to the destruction of the lower branches.

After a fire many geophytes become very prominent for a time and take a prominent place in the early development of the vegetation. Many of the most prized of the so-called Cape bulbs only flourish and produce their flowers after a fire, for example, various species of *Gladiolus*. *Watsonia rosea* and other species are abundant and form a very noticeable aspect with their conspicuous flowers in the second season after a fire. Following a fire a number of annual plants become prominent and abundant. Generally annuals are not a conspicuous part of this flora. After these annuals and geophytes, herbaceous plants attain an important place in the vegetation¹. The most abundant are tufted cyperaceous plants and a few grasses such as *Danthonia macrantha* and *Andropogon hirtus*. Along with them are a number of herbaceous or sub-shrubby plants in considerable variety. Gradually, if no other fire disturbs the progress, a decidedly xerophytic community in which Restionaceae play the most important part, becomes established. The Restionaceae are associated with a number of ericoid or xerophytic shrubs which have arisen from seed or sprouted from shoots, among the commonest of which are *Pelargonium cucullatum*, *Rhus lucida*, *Erica imbricata*, *Aspalathus divaricata*, *Penaea mucronata*, and especially *Anthospermum aethiopicum*. Gradually the under shrubs and the ericoid type of shrub assume dominance and these in turn are invaded by the larger bushes and the climax is re-established.

On exposed granite slopes on the western side a series of stages differing in some features can be traced. The Restionaceae and Cyperaceae here never attain the prominence they do on other parts, and especially on the more sandy soils. Instead, *Elytropappus rhinocerotis*, the rhenoster bush, becomes exceedingly abundant or even quite dominant after fire. This plant is one of the commonest in the south-western region as a whole and especially so in the burnt areas. After fire its spread is entirely from seed. On these western granite slopes the rhenoster communities become invaded gradually by other shrubs and especially by *Cliffortia ruscifolia*, *Metalasia muricata* and *Blaeria ericoides*. These and others gradually attain increasing control and drive out the earliest species, but are themselves invaded and dominated by *Protea lepidocarpodendron*. One other series may be noted which occurred on a steep granite slope with much sandstone talus on a western exposure. Here the first stage after fire was a mixed community in which *Watsonia rosea*, *Bobartia spathacea* and *Anthospermum aethiopicum* were especially abundant along with some grasses and restionaceous plants. Gradually bushes became established and a mixed community developed in which the most abundant plants were *Euryops abrotanifolius*, *Anthospermum aethiopicum*, *Rhus lucida*, *Osteospermum moniliferum* with *Metalasia muricata* and some *Leucadendron adscendens*. This mixed shrub community became invaded by *Leucadendron plumosum* which

¹ Cf. Levyns, 1924.

spread from seed and assumed the dominating rôle. This was more slowly followed by *Protea lepidocarpodendron*. I am informed by several observers that the present great abundance and spread of *Leucadendron plumosum* on these slopes is a phenomenon of recent date and that 10–12 years ago this plant was rare and of very local occurrence.

These various successions of regeneration after fire are dependent on the local conditions as to soil, etc. Some of the features of the soil during the process are worthy of note and are given in the following table:

A. Sandy soil	% humus	pH
1. Open Geophytes and Cyperaceae	3.4	4.0
2. Restionaceae	5.1	4.25
3. Ericoid shrubs	9.6	5.75
4. Climax	9.5	5.75
B. Granite soil		
1. Rhenoster	3.5	6.5
2. <i>Metasia</i> and <i>Blaeria</i>	3.95	7.0
3. Ericoid shrubs	5.4	5.5
4. Climax	6.4	6.25
C. Granite with sand		
1. <i>Bobartia</i> and <i>Metasia</i>	5.0	7.0
2. Mixed shrubs	7.9	6.75
3. <i>Leucadendron plumosum</i>	8.2	6.5
4. Climax (not yet developed).		

The series of communities that have been mentioned are those that follow a single fire, but it very often happens that other fires destroy the vegetation before the climax is reattained. Fires may destroy the vegetation at any stage and result in many complications and variations in the attempts at redevelopment. The effects of fires and especially of recurrent fires are the impoverishment of the soil by reduction of humus, the increase in the liability to drought in summer and soil erosion in winter. The effects of fires in these directions are to some extent cumulative and tend to become more pronounced¹. For example, plants sprouting from the stool after fire are killed by a recurrent fire that destroys the young shoots, and seedlings are destroyed before the flowering period. These and other results bring about the production of other kinds of community under such conditions, and especially of communities in which phanerophytes, and especially the ericoid shrubs, play a quite subsidiary part. Geophytes and hemicryptophytes are more resistant to fires. Many communities on these lower slopes in which Restionaceae predominate owe their existence to a succession of fires. On the more sandy soils the successive fires cause a great reduction of humus, the percentage falling as low as 2.4, and a great reduction in the water-holding capacity. For example, the saturation point of such a soil was found to be 28 per cent. of the dry weight while on an adjacent part that had escaped burning for some years it was 50–60 per cent. On such sandy soils the plant which obtains possession after fire is *Aspalathus chenopoda*, a shrubby plant with small pointed leaves. This may

¹ Cf. Larsen, 1925.



FIG. 5. Climax community on plateau. In foreground dense growth of ericoid shrubs, *Protea spicata*, *Leucodendron concolor*, *Watsonia tubularis*.

FIG. 6. Part of same locality as Fig. 5, five months after a fire. *Watsonia* very abundant.



FIG. 8. Burn successions on plateau. In background community of Restionaceae on black sand. To right in front, vegetation three years after fire, *Helipterum spicatosissimum* in flower. On left a recent fire.



FIG. 7. Succession after fire on lower slopes. In foreground *Metastasia muricata*, *Euryops abrotanifolius*, *Rhus lucida*, etc. Behind, advancing bushes of *Leucodendron plumosum*. The dark bushes are *Rhus*.

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form almost pure communities that only gradually become invaded by other plants such as *Pelargonium cucullatum*, *Montinia acris* and others. Some grasses and annuals and rather weedlike herbs also occur. Gradually these pioneers become ousted by *Lobostemon glaucophyllus*, *Metalasia muricata*, *Anthospermum aethiopicum* and some Restionaceae, especially *Elegia juncea*. The community which finally becomes established is characterised by an abundance of restionaceous plants and a number of small bushes, among which there is a marked absence of Ericaceae and of ericoid shrubs in general.

On shallower soils, and especially on the granite soils, the communities appearing after recurrent fires are composed very largely of herbaceous plants, among which *Bobartia spathacea*, *Tetraria ustulata*, and *Danthonia macrantha* are especially abundant. Where fires are very frequent, an open community results in which *Bobartia spathacea* is the characteristic and very much the most abundant plant.

There are many other communities of small xerophytic shrubby plants of various kinds which are the result of fires at varying stages of the development. Indeed, the great variety of communities that are found on these slopes is a result of the frequent occurrence of fires.

In any of these communities that form stages in the regrowth after fire there may be present individuals or islands of plants that represent survivors of the previous plant covering.

Plateau.

The habitat conditions on the plateau are somewhat different from those on the slopes. The underlying rock is sandstone, the beds of which are almost horizontal. The soil formed is always sandy but differs very much in depth. Where hard beds of sandstone are at the surface a very shallow soil results which often contains a high percentage of humus. Deeper soils are found over softer beds and on escarpments and talus slopes or the deltas of drainage channels.

As was noted earlier, there is more moisture available both from the higher rainfall and the prevalent mists. This is evidenced by the large number of stream channels, many of which have running water for much longer periods than is the case below. The soils, too, tend to accumulate greater quantities of humus: the surface soil is frequently quite black and in some cases a definite surface layer of sandy peat is formed. The soil below such a peaty surface is leached to a large extent. Practically all the plateau soils are distinctly acid in reaction.

In spite of these differences in the conditions the vegetation bears a strong general resemblance to that on the slopes in structure, form, and development¹. The stature of the plants is smaller, and Monocotyledons, and especially the Restionaceae, are very much more abundant. The great amount of the

¹ Cf. Engler, 1903.

Restionaceae gives a marked character to the vegetation of the plateau both in form and colour.

The plateau communities can be divided into three groups: (1) communities on sandy soils; (2) those on exposed horizontal sandstones; and (3) the communities of flushes and sheltered spots under cliffs, etc.

Communities on Sandy Soils. The community that can be regarded as the climax here is one made up of a considerable variety of shrubs, the majority of which have ericoid leaves. This is the most complex community and all the lines of development in the vegetation lead up to this. The actual constitution of this climax varies with the soil, slope, exposure, and other factors. In its most luxuriant form the shrubs produce a very dense growth of 3–4 ft. (1–1.5 m.) in height. While the ericoid is the prevailing leaf type, plants with larger leaves are present. Among these are *Leucadendron concolor* and *L. salignum*, which are locally abundant or even dominant. *L. salignum* is especially abundant where the climax has been reattained after destruction by fire.

The soil in this climax is quite black in colour and has a high percentage of humus, 50 per cent. or more.

There is not a very definite development of layers; the plants of smaller stature and of herbaceous habit occur between the bushes rather than below them. Lichens, some mosses, and a few geophytes form an underlayer. The population is a large one and varies from place to place. The following spectrum was obtained from an example on a sheltered slope with a S.E. exposure at an altitude of 2600 ft. (790 m.):

Total	M.	N.	Ch.	H.	G.	T.
78	7	42	19	18	12	0

The prevailing leaf form may be seen from the following percentages of the leaf-size classes of the larger plants:

Meso.	Mik-meso.	Mik.	Nano.	Lepto.	Compd.
2	4	23	17	40	13

Only a very few of the most characteristic plants can be mentioned. *Erica* is an important genus, among the abundant species of which are: *E. hispida*, *E. petiveri*, *E. coccinea*, *E. lutea*; also *Scyphogyne inconspicua*. *Berzelia lanuginosa* becomes almost dominant in the wetter parts. Other noteworthy plants are *Penaea mucronata*, *Cliffortia ruscifolia*, *Anaxeton arborescens*, *Protea cynaroides*, and a host of others. Among the herbaceous plants Restionaceae predominate with six or eight common species, *Aristea capitata* and *Watsonia tabularis* are also frequent.

This ericoid bush community, with its absence of annuals and its soil with a high percentage of humus, is the analogue of the *Protea* bush on the lower slopes. The differences are all such as are capable of correlation with the cooler and moister climate and the different types of soil. In structure and development there is a strong resemblance: the species of *Leucadendron* may be looked

upon as replacing the Proteas though they never become so abundant. On the other hand, in many features this community is directly comparable with the Heath communities of Europe: in the type of habitat, humus content of the soil, leached subsoil, life form, and structure.

This climax is often destroyed by fire and its regrowth can be traced. The effects of burning and many of the stages of regrowth are very similar to those already described. Very few of the ericoid shrubs sprout from the bases; this does happen in some of the plants, e.g. *Berzelia*, *Penaea*, *Protea cynaroides* and some others. The behaviour of the hemicryptophytes and some of the chamaephytes depends on the intensity of the fire and on the moisture conditions at the time. When a fire follows a damp period, only the upper portions of these plants are destroyed and they sprout up directly. But a more intense fire, and especially one following a drought period, does much more damage, most of the plants on or near the surface are killed and much of the humus is consumed. Severe soil erosion often results also due both to wind and to rain.

In any case, after a fire there is a temporary increase in the geophytes, which form a marked and characteristic phase. The effects are in some cases quite remarkable; only one example need be quoted, *Cyrtanthus angustifolius*. This plant flowers abundantly immediately after a fire, though at other times it remains entirely vegetative and is very difficult to find.

The destruction of the plant cover allows an entrance for many plants that find no place in the mature vegetation. These are light-demanding herbs, grasses and others. Among them mention must be made of *Schizaea pectinata* which becomes very abundant and forms a good fire indicator.

After a severe fire these light-demanding plants, many of which are grasses or plants of grass-like habit, form pioneer communities with the geophytes. Such communities can be picked out from considerable distances owing to their paler, greener colour as compared with the dark shades of the climax and restionaceous communities around. On shallower soils and rocky places plants such as *Othonna parviflora*, *Senecio grandiflorus*, *Corymbium nervosum*, and others take the place of the grass-like plants.

Gradually the Restionaceae and Cyperaceae increase in importance and assume dominance in the intermediate stage of regrowth. The ericoid shrubs become re-established rather slowly among these plants.

On the plateau where fires have been frequent in their recurrence and especially where this has been long continued, the regrowth succession is altered. As on the lower slopes, so here to a greater extent, the humus is destroyed and much of the loose surface soil is removed. As a result regrowth is slow beyond a certain point which is rapidly attained. This is a community of low-growing plants. Tufted Restionaceae and Cyperaceae with *Corymbium nervosum* are the most characteristic. Small shrubby plants are present but not in sufficient quantity to give a definite character. Among the most abundant are *Anaxeton arborescens*, *Penaea mucronata*, *Psoralea aculeata*, *Hermas villosa* and *Thesium*

spp. An extremely characteristic plant here, and one at times very abundant, is *Tetraria thermalis*. This stands out among the small plants around with its large hard leaves and its very tall inflorescences. The rhizome, which is on the surface, is thick and protected by leaf bases and has great powers of resistance to fires.

This type of community is very common and, owing to its rapid regrowth up to this stage and the slow development beyond, appears almost as a stable community. A comparison of the spectra of this type with that of the climax is instructive.

	Total	M.	N.	Ch.	H.	G.	T.
Burn Comm.	54	0	10	32	42	16	0
Climax	79	7	42	19	18	12	0

Communities of this type show some variations in composition from place to place, but the general features remain the same and the type is easily recognised. It covers large areas not only on Table Mountain but also on all the mountains of the south-western district.

That this is not a true stable type can be seen by a study of the changes that occur where burning has been prevented for some time; humus is re-formed and small-leaved shrubs become much more abundant and spread at the expense of the hemicryptophytes.

Communities on Horizontal Sandstones. Over considerable stretches of the more level parts of the plateau the horizontal beds of sandstone form the surface. The plant covering under such conditions shows differences on the upper plateau as compared with the lower one: differences which are due to the increased moisture on the summit. The summit plateau, which has an altitude of 3000 ft. (900 m.) and upwards, will be described first.

These conditions afford a favourable opportunity for the study of the primary succession. On the rock surfaces soil accumulates slowly: it is first formed along cracks and joints, with the result that the appearance is presented of vegetation along straight lines with bare lichen-covered rock between. These lichens may be looked on as the pioneers in the succession¹, but the first plants that can be said to cause an accumulation of soil are mosses, and especially tufted mosses. These are of various kinds; the most generally abundant are species of *Campylopus*, *Grimmia*, *Macromitrium*, and of *Dicranum*. Under favourable conditions these mosses form a continuous carpet along the cracks and extend out over the rock surface. This moss mat has a high water-holding capacity and tends to the accumulation of a soil that has a high percentage of organic matter. Several small flowering plants obtain a nidus on this mat; *Utricularia capensis* and *Drosera cuneata* are abundant in wet places. The plant, however, which is mainly responsible for initiating the next phase in the succession is *Ursinia nudicaulis*. This is a plant with rosettes of leaves which grows on these mosses and gradually eliminates them. *Ursinia* is in its turn gradually suppressed by restionaceous plants which assume dominance

¹ Bews, 1916.

on the soil built up in this way. The actual species are rather numerous and vary with the conditions. The first-comers are tufted plants, those with more elongated rhizomes appear later. *Restio compressus* ultimately assumes dominance under moist conditions, but in drier places a mixed community is formed. Characteristic plants associated with these Restionaceae are *Chrysithrix capensis*, *Villarsia ovata*, and *Achneria capensis*.

As soil is formed by the activities of the plants in accumulating humus and weathering the rock, other plants make their appearance. These are largely small shrubs with ericoid leaves: among the more abundant are *Erica coccinea*, *E. pluckenetii*, *E. petiveri*, *E. empetrifolia*, and others, *Cliffortia ruscifolia*, *Penaea mucronata*, *Blaeria purpurea*, and occasionally *Brachysiphon imbricatus*. Along with these are smaller plants such as *Helipterum sesamoides*, and *Helichrysum grandiflorum*, and some geophytes. With increasing quantities of these ericoid shrubs and associated plants the vegetation approaches a community very similar indeed to the climax described above. The differences that occur can be correlated with the shallow soil and liability to summer drought. In the later stages, when this climax is approached *Erica lutea* is one of the prominent plants.

Where the soil is damp and is composed almost wholly of organic matter the communities of Restionaceae become firmly established and remain in a more or less stable condition for long periods.

The earlier stages of this succession appear as zones which tend to extend over the flat rock surface. The progress is limited by the water supply and is fluctuating. In a dry summer, such as that of 1925-6, for example, when there were very few S.E. mists, the moss edge is killed off in many places and the vegetation retreats.

The flora of these rock flats is distinctly a hemicryptophytic one. The following spectrum is based on lists of the flora on the "Western Table" at an altitude of 3300 ft. (1000 m.):

Total	M.	N.	Ch.	H.	G.	T.
54	0	26	18	40	14	2

The following table gives some indication of the changes that occur in the soils during the succession:

Community	% humus	pH	Water at saturation	(% of dry soil)
Moss and <i>Ursinia</i>	8.5	5.0	59.2	Soil very thin
Moss with Restion.	8.1	4.5	61.3	Dense vegetation
Restion. and ericoids	25.4	4.75	128.0	
Restion. and <i>Penaea</i>	26.1	6.0	152.2	Soil thin
Restion. and <i>Villarsia</i>	47.1	4.5	270.9	Dense vegetation in a rock hollow

Different succession phases are followed in wetter or drier parts. In hollows and by streams where permanent ground water is present, soil is formed more rapidly. Here the small pioneer plants become displaced by the very tall reed-like *Dovea mucronata*. This often forms pure communities on damp soil; by streams it is associated with *Berzelia lanuginosa* and on very wet soils with

Bulbinella robusta, *Leptocarpus paniculatus*, and others. On the other hand, under specially dry conditions, the mosses do not flourish and the early colonists are succulent plants, *Rochea coccinea*, *Mesembryanthemum* spp. and others. The soil which collects from the slow rock disintegration is colonised by xerophytic shrubs such as *Cliffortia ruscifolia*, *Chrysocoma coma-aurea*, *Erica diosmaefolia*, *E. petiveri*, and others. Species of *Restio* with a sprawling habit are often abundant and cover rock ledges. *Felicia aethiopica* and *Selago spuria* are abundant where shelter is provided. These communities occur on rock faces, on exposed rocks, and at the edges of the plateau. The succession here is very slow.

Where soil is formed more rapidly communities showing every stage of transition between those on the rock surfaces and those described earlier can be found.

These communities on the horizontal rock faces have been much less affected by fires than is the case with most parts of the mountain. Their escape is due to the discontinuous nature of the plant covering. The progress of a fire is stopped by the uncovered rocks. Where the vegetation has become continuous the effect of fire on plants on such thin soils is most pronounced: not only are most of the plants killed entirely, but the humus is consumed. In the regrowth a number of plants not present at all in the original communities make their appearance. A single example may be quoted in illustration. The original community was composed of Restionaceae with a considerable admixture of ericoid shrubs. Two years after burning a community of strikingly different appearance had developed: from a distance it stood out clearly pale green as contrasted with the dark unburnt portions. The most abundant plants were *Stoebe cinerea*, *Ursinia crithmifolia*, *Tetaria cuspidata*, with scattered tufts of *Danthonia macrantha*, and *Pentaschistis curvifolia*. Along with these were frequent plants of *Watsonia humilis*, *W. tabularis* and *Corymbium nervosum*. Restionaceae were very inconspicuous and shrubby plants practically absent. In some places *Ursinia nudicaulis* was abundant and apparently tending to reproduce the original succession.

Under the rather drier conditions of the lower plateau, the series of phases on this type of habitat is somewhat different. Mosses are very much less abundant and the soil formed contains much less humus. The pioneer stages are like those on the driest portions at the higher levels: plants with succulent leaves preponderate. Those that follow are xerophytic shrubs, among which *Cliffortia ruscifolia*, *Chrysocoma coma-aurea*, *Metalsia divaricata*, and *Cullumia ciliaris* may be mentioned as abundant in the early stages. Later, other plants, including geophytes such as *Agapanthus umbellatus*, and *Watsonia tabularis*, become established, though the community remains one in which shrubby forms predominate as is seen from the following spectrum:

Total	M.	N.	Ch.	H.	G.	T.
57	0	32	23	26	17	2

This spectrum forms a marked contrast to that from the upper plateau for communities under parallel conditions.

Flushes and Sheltered Rocks. On the plateau where shelter and permanent moisture are provided communities of a different general facies are developed. Such communities are of frequent occurrence but in most cases are of limited areas and their development and succession phases have not been studied in any detail at present. These are distinguished by their much less xerophytic character. The average leaf is much larger and much thinner, indeed, often typically mesophytic. Where fully developed, the community forms a dense growth of shrubby plants and large herbs among which very abundant members are: *Cliffortia odorata*, *Osmitopsis asteriscoides*, *Todea barbara*, and several species of *Erica*. *Senecio verbascifolius* is abundant on sheltered rocks with a thin but wet soil. A plant of not uncommon occurrence in this kind of habitat is *Cunonia capensis* which is found up to a height of 3300 ft. (1000 m.). On the plateau this plant grows as a large shrub rather than a tree. Along with these there occur many of the more moisture-demanding species of the communities already mentioned, and many small plants which require continuous water supplies, mosses, ferns, orchids, small species of *Erica*, *Kniphofia*, etc. Moss-covered rock flushes form the habitat of some of the more showy species of *Disa* and other much prized plants.

While every stage of transition can be found between these communities of broad-leaved almost hygrophilous plants and those of the open parts, the extreme form appears quite distinct both in structure and development.

Cliffs and Rock Ledges. Sandstone cliffs occur on all sides of the mountain; they vary very much both in height and steepness. The plant populations of these cliffs for the most part are those of the drier portions of the upper parts of the mountain. They can be regarded as representing stages in development that are prevented from advancement beyond an early phase by the lack of soil and physiographic features. In addition to absence of soil, the plants have to withstand the recurrence of periods of considerable drought. Correlated with this is the presence of a number of succulent plants that act as pioneers, e.g. *Mesembryanthemum* spp., *Othonna arborescens*, *Senecio crassulifolius*, *Cotyledon hemisphaerica*, *Crassula* spp., etc. In addition there are a certain number of plants that have their most characteristic habitat here and may be regarded almost as chomophytes: e.g. *Euryops pectinatus*, *Coleonema album*, *Helichrysum* spp., etc.

The most general vegetation is composed of xerophytic shrubs, of which *Cliffortia ruscifolia*, *Coleonema album*, and *Euryops abrotanifolius* are very abundant. The communities, however, show great variations in accordance with the exposure and the moisture conditions. On sheltered cliffs, even on the exposed sides of the mountain, quite a number of shade plants are found and even forest trees. For example, on the south face of a buttress on the western side of the mountain numerous bushes and small trees were present. Of

26 woody plants found here, 7 were forest trees, 7 shrubs associated with the forest; of the remainder 9 were typical sclerophylls and 3 plants found on the plateau. Numerous smaller plants also occurred which likewise included shade plants, succulent chomophytes and others. Without going into any details, this example will serve to illustrate the features of the vegetation of these cliffs. On them there occur phases of development of all the communities of the sandstones. Owing to the nature of the habitat these communities are of very limited extent, and, except quite locally, development does not progress beyond the earlier stages. Wherever a possibility of advance, however, is given, indications of the later stages are present. The actual plant groups that occur are small fragments of communities from very many phases of the successions, each determined by the local conditions, and together forming a very mixed assemblage.

FORESTS.

Forest communities occur in the deeper ravines and kloofs on all sides of the mountain. The fullest development is attained on the sheltered eastern side and in the deep kloofs on the south; here the forest extends beyond the confines of the ravines on to the open slopes¹. On the more exposed sides, except for a few isolated patches, forests are confined to the stream beds. Forest is also found on the plateau in the shelter of steep cliffs up to an altitude of 2300 ft. (700 m.).

The forest forms a community in marked contrast to any of those so far considered, both in the plant form and also in the leaf-type and floristic composition. Instead of the small xerophytic, dull-surfaced type of sclerophyll leaf, the trees are characterised by the possession of evergreen elliptical leaves with a dark polished surface. These leaves are typically glabrous, at any rate on the upper sides, and are simple. A few have compound leaves, e.g. *Cunonia capensis*, but in such cases the leaflets conform to the general type. The size varies, but the average is distinctly larger than the sclerophylls. The following are percentages of the leaf-size classes of the forest trees:

Total	Meso.	Mic-meso.	Mic.	Nano.	Lepto.	Compd.
34	12	21	56	3	0	9

Of these 34 species, 4 only have hairs on the upper surface, and only 1 has stomata on the upper side. This plant, *Gymnosporia buxifolia*, is one that occurs in a great variety of habitats and is by no means confined to the forest communities. On the other hand, of 25 flat-leaved sclerophylls from the *Protea* bush, 14 had stomata equally distributed on both sides.

The texture of the leaves of the trees varies but is in most cases thinner than the sclerophylls and this is especially the case with the more water-demanding trees. Deciduous trees are rare; the only truly deciduous tree is *Celtis rhamnifolia*, which has a very restricted distribution here².

¹ Cf. Marloth, 1908.

² L. Bolus, 1923.

In these forests no single tree can be said to be dominant. The canopy, which is dense and continuous, is made up by a considerable variety of species¹. The external level of the canopy is markedly irregular, some trees attaining a greater height than others. The composition of the forest varies with the degree of moisture: on the wettest parts *Cunonia capensis* is the most abundant and may form locally pure stands, while in drier conditions *Olea capensis*, *Podocarpus latifolius*, *Olinia cymosa* and *Elaeodendron capense* are the most abundant. The largest leaved trees, *Curtisia faginea* and *Ocotea bullata*, occur mostly as undertrees. This is at any rate in part due to felling; both of these are valuable timbers and of slow growth. Felling is also accountable for the comparative rarity of *Olea laurifolia* and the absence of large trees of *Podocarpus latifolius*. Both of these are exceedingly characteristic trees in the forest of the south coast regions.

Undertrees are a feature of these forests and add to the density of the canopy: such plants as *Halleria lucida*, *Maurocenia frangularia*, *Scutia indica*, and others are confined to this layer. Shrubs as such do not form a definite layer and are often conspicuous by their absence, except in openings in the canopy where they are numerous and varied. Shrubs occur along streams in the forest.

In the moister parts lianes are of frequent occurrence: *Secamone alpini*, which has polished leaves of the same type as the trees, and *Rhoicissus capensis*, with large thin leaves, are the most abundant. Both of these form woody climbing stems that festoon the tree stems and branches forming what are popularly known as "monkey ropes."

The undergrowth varies with the soil, moisture, the degree of exposure and of shade. The plants are herbaceous, not shrubby, and mesophytic or even hygrophytic. Amongst the commonest are: *Knowltonia vesicatoria*, *Antholya aethiopica*, *Schoenorhaphium capense*, *Nemesia lucida*, and *Zantedeschia aethiopica*. Ferns are exceedingly abundant in the wetter parts and occur in considerable variety, including the tree-fern *Hemitelia capensis* and several filmy ferns². On wet rocks, in addition to filmy ferns, there are numerous bryophytes and *Peperomia retusa*.

Epiphytes are not infrequent on the tree stems though the number of species growing in this way is not great. *Polypodium lanceolatum* is the most frequent, but several of the rock-growing plants may occur as epiphytes.

The following are spectra based upon lists of forests on the eastern side of the mountain above Kirstenbosch. The first is a general list while in the second those plants that only occur in openings or at the margins, are excluded:

Total	MM. & M.	N.	Ch.	H.	G.	T.	E.
117	38	20	5	22	11	2	2.5
86	45	10	1	28	14	0	3

The forests on the northern and western slopes of the mountain are much

¹ L. Bolus, 1923.

² Cf. Compton, 1924.

more limited in extent and, with very few exceptions, are strictly confined to the ravines. They are of exactly the same type but are less luxuriant and without many of the more markedly hygrophytic features. Ferns are much less abundant, tree ferns are wanting, and lianes and epiphytes are scarce or absent. There is less variety among the trees and the larger leaved species are wanting.

Forests of a still more xerophytic type occur on the exposed sides, here and there, on boulder talus. These are small isolated patches. In them the dominating plants are small trees or even large bushes not more than 12–15 ft. (3.5–4.5 m.) high. The larger patches are very dense and difficult to penetrate. The trees are the most xerophilous species: *Olea verrucosa*, *Elaeodendron capense*, *Maurocenia frangularia*, and others, and are accompanied by a number of bushes which only occur at the margins of or outside the main forests. Lianes are absent except for scrambling *Asparagus*, and epiphytes are only represented by numerous lichens. Owing to the nature of the substratum, boulders, and to the dense shade, ground vegetation is limited in quantity though true shade species do occur in crevices.

The forests in the sheltered spots on the plateau are of a very similar nature to those on the slopes. They occur on boulder talus. Most of the typical forest trees are present with the exception of the most hygrophilous. In these plateau forests *Podocarpus latifolius* is very abundant, more so than on the slopes. Whether this is a real difference or is the result of the cutting out of this tree in the more accessible places is at present rather an open question¹. *Podocarpus*, either alone or associated with some other trees, occurs frequently in small patches in shelter up to 2700 ft. (820 m.) especially among boulders, or by streams. In the forests proper and in these small patches there is a shade ground flora with many ferns.

A comparison of the floras of these forests in various situations reveals the fact that the only species that occur in the more exposed places which are not found in the main forest may be looked upon as invaders from sclerophyll communities. The trees composing the forests in the more exposed situations are those found in the driest parts of the main forest and especially at the margins. For example, at Kirstenbosch, the edge of the forest that extends beyond the ravine is characterised by an abundance of *Elaeodendron capense*, *Olinia cymosa*, *Maurocenia frangularia*, and others. These trees, with *Olea verrucosa*, are the chief constituents of the forests on the more exposed slopes. These, and other points, which need not be elaborated, lead to the conclusion that the more xerophytic type of forest represents a stage in the succession that culminates in the hygrophilous type. Under the dry conditions on the north and west slopes the ultimate climax cannot be attained, except in a few situations where permanent ground water and a great degree of shelter are provided.

¹ Cf. Bews, 1916.

There is no doubt that the forests that exist on the mountain to-day, represent only the remains of a once much more extensive community¹. Evidence for this can be got from many sources. For example, on the slopes of Orange Kloof there are isolated patches of forest separated by simpler communities but with no distinct change of habitat conditions. Again, at Kirstenbosch, some of the ravines are completely filled by forest, while others, with apparently identical conditions, contain only isolated patches or strips of trees. Indeed, on practically any part of the mountain, evidence of the former greater extension of forest is obtainable. Destruction has been due to felling to some extent but fire has been much the most extensive and complete agent and especially so on the upper portions.

On the lowest slopes ground that may at one time have been occupied by forest is now largely taken up by alien trees, either in plantations or in self-sown communities derived from originally planted trees. These are considered later.

Native vegetation that occupies ground at one time held by forest is of many kinds. Where fires have been severe and frequent the forest has totally disappeared and its place has been taken by sclerophyll communities. There are places, however, where there is evidence of a regrowth of the vegetation towards forest. As a marginal zone to forest patches, and along streams where forest does not now occur, there is a community that can be regarded as a forerunner of forest. This is made up of bushes of large size, and decidedly less xerophytic than those of the *Protea* bush. Characteristic plants are: *Podalyria calyptrata*, *Cluytia pulchella*, *Phylica buxifolia*, *Gymnosporia laurina*, *G. buxifolia*, *Polygala myrtifolia*, *Pelargonium cucullatum*, *Rhus tomentosa*, and *Cussonia thyrsiflora*, with several others. Along with these bushes are many smaller plants which are very characteristic: *Senecio rigidus*, *Salvia aurea*, *Leonotis leonurus*, *Lobostemon montanus*, and in rocky places, *Arctotis aspera*, to mention only a few. Several bushy plants typical of the sclerophyll communities occur here also but never approach to dominance over these less xerophytic species. The following percentages of the leaf-size classes of this kind of community will help to emphasise its distinction from any of those of sclerophylls:

Meso.	Mic-Meso.	Mic.	Nano.	Lepto.	Compl.
3	9	28	28	3	28

This community is very dense and little light penetrates to the ground, and undergrowth is almost confined to spaces; in these there occur *Antholysa aethiopica*, *Knowltonia vesicatoria*, *Zantedeschia*, and many of the less hygrophilous shade plants.

Climbers and scramblers are rather abundant in this community and these with the dense growth of the bushes produce a thicket by no means easy of penetration. The commonest climbers are plants with herbaceous stems among

¹ Cf. **Theal**, 1882; **Marloth**, 1908.

which mention may be made of *Microlooma sagittatum*, *Cissampelos capensis*, *Fagelia bituminosa*, species of *Asparagus*, and the ubiquitous *Cassytha capensis*; *Cuscuta africana* is also common.

When this community is dense and extensive, forest trees occur among the shrubs. *Olea verrucosa*, *Olinia cymosa*, and *Elaeodendron capense* are the most abundant but *Royena lucida*, *Hartogia capensis*, *Rapanea melanophloios*, and *Maurocenia frangularia* also occur. The presence of these trees, together with the distribution of this community, seem clearly to point to its being a stage in the re-establishment of the climax.

As might be expected, it is on the more sheltered side of the mountain that the most obvious stages of forest regeneration can be traced. This shrub community becomes very luxuriant and tall and the undergrowth has an abundance of *Pteridium aquilinum*. Another plant that is especially frequent along streams is the tree *Virgilia capensis*: this with *Podalyria calyptrata* forms a woodland of light canopy beneath which many shrubs and other plants flourish; especially abundant are *Plectronia ventosa*, *Psoralea pinnata*, and *Gymnosporia buxifolia*. Exceedingly similar communities of *Virgilia* form forerunners of the forest regeneration at Knysna where the forest climax is the dominant vegetation type.

These shrub communities, though stages in the forest regeneration, are not the pioneers after destruction by fire. The earlier stages can be traced on parts of the sheltered side of the mountain where forests have been recently destroyed. The first communities to develop are composed of a mixed assemblage of herbs and undershrubs among which *Pelargonium cucullatum*, *Aristea capitata*, *Cliffortia odorata* and *Pteridium aquilinum* are prominent. Into this community *Podalyria* and other shrubs invade and gradually become established. *Widdringtonia cupressoides*, though a marginal plant in the forests, is prominent in these regeneration communities. It has considerable power of fire resistance, sprouting from the stool when the upper parts are killed.

Evidences of a primary succession to forest are rare but one example may be quoted. This occurs on the ridge of boulders on the east side of the mountain that provides the habitat for *Aloe succotrina*. Here, as was noted by Marloth¹, the forest is extending over the boulders. These become covered by lichens and mosses and on these several shade-loving species become established. The trees obtain a foothold in the clefts between the rocks; those that are advancing here are chiefly *Canonia capensis*, associated with *Cluytia pulchella*, *Gymnosporia buxifolia* and other bushes. *Olea verrucosa* also occurs here.

The *Aloe* apparently represents a pioneer stage; at any rate it is being killed off by shade in its original habitats. A comparison of a photograph taken here in 1908 by the late Prof. Pearson with the present appearance affords very clear evidence of the recent advance of the trees.

¹ Marloth, 1906.

PLANTATIONS AND ALIEN PLANTS.

There is no necessity to enter into any details in regard to these. The basal slopes on the northern and western sides of the mountain have been very largely occupied by non-indigenous trees. By far the most abundant are *Pinus pinæa*, *P. pinaster*, and *Quercus robur*. The last is in ravines or quite at the base. Plantations, chiefly of *Pinus pinaster*, have also been made round the reservoirs and at other places on the plateau. Other trees planted on the slopes are *Pinus halepensis*, *P. insignis*, and other species, also several species of *Eucalyptus* and of *Acacia* though these are much less extensive than the conifers.

The planted trees grow fast and soon eliminate the native vegetation. Some of the geophytes, *Ornithogalum*, *Albuca*, *Ferraria*, *Moraea*, etc., hold their place but with few exceptions the larger native plants will not withstand the shading and are driven out. *Myrsine africana* persists to some extent but most of the native shrubs are confined to openings in the canopy.

Some of the introduced trees are spreading out by self-sown seeds: this is notably the case with *Pinus pinaster*, and rather less with *P. pinæa*. This spread from seed is often very rapid and these trees are in many places tending to dominate and drive out the native flora in stations near planted or established trees. This spread is certainly assisted by the reduction in competition brought about as the result of fire. The climax and more complex communities appear able to withstand the pines. The distance travelled by the pine seeds is not great; seedlings have only been noted in the vicinity of parent trees.

Pinus pinaster occurs on the summit of Table Mountain, but its presence here is a relic from a plantation on the plateau which was destroyed by fire some years ago. The few survivors are now producing seed and spreading locally.

Pines are not the only non-indigenous plants that are spreading at the expense of the native vegetation. Another that is doing so is *Hakea*. The original introduction of this plant has a less obvious object but it is certainly one that has come to stay. Three species are present on the lower slopes of which *H. pectinata* is the largest, commonest and the most important. This plant is spreading rapidly on the western side from sea level up to about 1200 ft. (360 m.). It is a large, rapidly growing bush that flowers and fruits very freely. In parts it has formed closed communities from which all other plants are excluded. Elsewhere it spreads into the native communities and its rapid growth enables it to overtop its competitors and maintain a firm hold.

In several places *Hakea* and *Pinus pinaster* are competing with the native shrubs in areas recovering from fires. The much more rapid growth of the aliens renders their ultimate domination the probable result.

The spread of *Hakea* is assisted by fire. The extremely resistant fruits open after burning and the seeds germinate at once.

The much smaller *Hakea acicularis* is spreading fast on the lower slopes on the sheltered side, but at present it does not appear likely to attain dominance.

An investigation of the spreading and general behaviour of *Hakea pectinata* is at present in progress.

Several other introduced trees and shrubs are spreading but to a much more limited extent: *Albizzia lophantha*, *Acacia cyclopis*, *A. decurrens*, *Populus canescens*, and *Genista canariensis* are examples.

Of the herbaceous and smaller introduced plants little need be said. Few of them have extended beyond the immediate vicinity of disturbed land. A few grasses have, at any rate temporarily, established themselves on the ground disturbed in the works carried out in the building of the reservoirs on the lower plateau: *Dactylis glomerata* and *Holcus lanatus* are the most abundant.

GENERAL CONSIDERATIONS.

From the foregoing account it will be apparent that in many features the existing vegetation of Table Mountain has been very considerably altered as compared with what must have been its original condition. This alteration is shown in many features and evidences can be obtained from many sources. Of the most obvious features it will be sufficient to mention the almost complete occupation of the lowest slopes on the north and east sides by foreign trees and the accompanying disappearance of the native flora, and on other parts the very small area occupied at present by the climax communities. This in itself, on an ancient and stable land surface, is evidence of destructive change. In an attempt to reconstruct the original vegetation, very little assistance is to be obtained from the rather meagre descriptions of the older botanical travellers, though these do give some indications. Thus Burchell¹, writing in 1810, describes *Aulax* and other shrubby plants growing at the top of Platteklip gorge on the top plateau where they certainly do not grow at present. Again, Bunbury² in 1838 mentions especially the abundance of *Disa uniflora* on the summit plateau where, at present, he would be a lucky person who could find a single specimen. These and other observations that could be quoted all tend to confirm the great amount of change that has occurred.

As has been emphasised, by far the most effective agent of change has been the frequent burning of the vegetation. The effects of this need not be repeated; they result in the retrogression of the normal succession and an impoverishment of the flora. Other factors have operated also. Picking and uprooting of flowers or plants for sale has undoubtedly caused a retreat of many of the more conspicuous plants to the less accessible regions but has not been sufficiently extensive to alter the character of communities.

Grazing of cattle and goats is a more important factor and one which has increased considerably in intensity on the lower slopes in recent years. This, again, tends to prevent the development of the communities of the later phases of the succession and encourages hemicryptophytes and others with greater powers of vegetative propagation as opposed to the shrubs. Another factor

¹ Burchell, 1822.

² Bunbury, 1848.

which has caused not inconsiderable change is the cutting of timber and firewood. A marked feature of all the sclerophyll communities is the absence of trees. This has been discussed fully by Marloth¹ and there is no reason to doubt his view that the absence of trees is very largely artificial. Many of the dominating plants of the climax can attain tree stature, *Protea grandiflora* and *Leucospermum conocarpum*, for example, and the more xerophytic forest trees might occur in this community. Indeed relics of such tree growth are still to be found.

As regards the vegetation, when full allowances have been made for the alterations and modifications that have been brought about, a general uniformity in type is clear². The growth forms and physiognomy of both climax and developmental stages are very similar from base to the summit of the mountain. In each case the climax is a bush community of the hard-leaved sclerophyll type though the ericoid leaf is very frequent or even dominant in the upper regions.

The comparison between this vegetation and that other sclerophyll region has often been made^{1,3} and the similarities between the vegetation of the lower slopes especially and the *Macchia* of Corsica⁴ and the Chaparral of California⁵, for example, is most striking. This comparison has been accepted generally as representing a real unity of type, as is shown by the use of the term "*Macchia*" for these communities⁶. The second type of vegetation on these slopes, Marloth's "*Hügelheide*," is on a different basis. This is definitely composed of developmental stages that culminate in the "*Macchia*." The distinction between "*garigues*" and "*macchia*," here, that is made by Warming and Graebner⁷ is also merely a separation of seral communities.

While the similarities are very striking there are many points of difference, so many indeed, that it is perhaps inadvisable to introduce the Mediterranean term "*Macchia*" for the South African communities. If a vernacular term is needed the local name of "*Fynbosch*" is more suitable.

As compared with most of the other sclerophyll regions, the absence of tree growth is a decided feature. While this is partly secondary, it is still exceedingly improbable that forest growth was ever general as is the case in Australia⁸ and in many parts of the western Mediterranean⁹.

The communities on the plateau, while possessing strong similarities of type yet exhibit many distinctive features. The climate in which they develop is considerably more humid than that typical of sclerophyll vegetation. This allows a much greater accumulation of humus in the surface layers of the soil, and further, results in the predominance of the ericoid and reed types of life

¹ Marloth, 1908.

³ Schimper, 1898; Grisebach, 1878, etc.

⁶ Cooper, 1922.

⁷ Warming and Graebner, 1918.

⁸ Diels, 1906; Adamson and Osborn, 1924.

² Cf. Engler, 1903; Drude, 1897.

⁴ Rikli, 1903.

⁵ Marloth, 1908; Bews, 1916.

⁹ Tansley, 1912.

form. In all these features this vegetation shows a distinct approach to the conditions in the Heath types in northern and western Europe. It occupies a position and structure intermediate between the typical sclerophyll and the heath of the cool oceanic climate. There seems no logical reason for the separation of the open communities of the plateau (the "Fellfield" of Bews¹) which are earlier stages of development often prevented from advance owing to the edaphic conditions.

The question of the relationships of the forests to the sclerophyll communities on the one hand, and to those of other regions on the other, is a more disputed one. The majority of writers have considered these forests as belonging to a wholly different vegetation type or formation² from the *Protea* bush and its associated communities. This is the view taken up by Marloth³, Schimper⁴, Drude⁵, and more recently by Shantz⁶. These forests are very different from the sclerophyll forests of other regions and indeed may be said to possess no sclerophyll characters at all in their full development⁷. They have an entirely different leaf form and are much more hygrophilous in nature. Their flora too is quite different from that of the sclerophyll communities. The comparison with "Laurel" forests⁸ or with subtropical rain forests⁹ is certainly much closer. The distinction in form, structure and population applies not only to the forest climax but also, to a large extent, to those communities that are regarded as stages in the development. On the other hand, there is no doubt that forest at one time occupied habitats that are now covered with typical sclerophyll communities. Also there are many traces of developmental phases of forest or allied non-xerophytic communities at various places in the sclerophyll region. This must not be taken to imply that the sclerophyll vegetation would ultimately advance to forest. It rather indicates that the climatic conditions existing on Table Mountain are such that any increase in moisture either from springs, shelter or otherwise, introduces a climate favourable to forest. In other words, the climate here is almost intermediate between that producing a typical sclerophyll climax and that of the forest climax. This is emphasised by a comparison of Table Mountain with the mountains further inland when it appears that the communities here, except for those on the most exposed sides, are less xerophytic and more luxuriant. The climate of Table Mountain as compared with the mountains on the mainland is tempered both by its high rainfall and by its proximity to the sea which gives a higher average humidity and results in very frequent summer mists. The sheltered side of the mountain especially has a climate much more humid than that supporting a true sclerophyll vegetation and this is reflected in the luxuriant communities and prevalence of forest. The limitations of forest area and the

¹ Bews, *l.c.* ² Clements, 1916. ³ Marloth, *l.c.* ⁴ Schimper, 1908.

⁵ Drude, 1897.

⁶ Shantz and Marbut, 1923.

⁷ Schimper, 1898, 1908; Drude, 1897; Tansley, 1912; Cooper, 1922; Diels, 1906.

⁸ Warming and Graebner, 1918.

⁹ Schimper, 1908.

establishment of communities of the sclerophyll type after their destruction are both explainable by the same causes. When a forest is destroyed by fire or by felling, the resulting removal of cover allows increased desiccation, oxidation of humus, an increase in water run off, and soil erosion. These factors acting together may well limit the redevelopment of the more hygrophytic type in conditions that are always near the limit of dryness for it.

The extreme view expressed by Hardy¹ that the whole of the slopes were at one time clothed with forest and that all the shrub communities have developed after its destruction is much too sweeping. There is no evidence that the forest ever extended beyond the kloofs and ravines and a few especially favoured spots on exposed sides of the mountain. The climax here, as has been mentioned, did probably contain, once, plants of tree form, and included some of the most xerophytic of the forest trees, but the presence of these cannot be taken to indicate that the succession would ever advance beyond a tall bush community of the type described. Even on the sheltered side of the mountain there is not any evidence obtainable that the *Protea* bush undergoes development to forest. This community undoubtedly shows many points of similarity with the communities leading to forest, in the presence of many shade plants and plants of mesophytic rather than xerophytic structure. The development from some of the earlier phases may proceed towards one or other of the climax communities according to the local climatic conditions, but when the more complex sclerophyll communities are developed, even the most sheltered forms of them, the forest series does not appear capable of invading them. There is, of course, a transition zone, where mixed communities are developed between the two.

The parallel development of scraps of forest and of sclerophylls on the cliffs which was described, further indicates how close the conditions on the mountain are to those necessary for each of these types.

The communities of broad-leaved plants in shelter and by flushes that occur on the plateau seem to bear the same relation to the heath-like communities that the forests and the associated types do to the sclerophyll communities on the slopes. They represent a development under conditions more continuously moist in climate.

SUMMARY.

1. The vegetation can be divided into three types or formations: a sclerophyll type on the slopes, the climax of which is a xerophytic bush community characterised by an abundance of even dominance of the larger Proteaceae. Several forms of this are noted with varying dominants: *Protea lepidocarpodendron* on exposed slopes, *Protea incompta* on sheltered ones, *Protea grandiflora* on sandstone talus, *Leucospermum conocarpum* on sandy soils and boulders, and *Leucadendron argenteum* on deep soils, mostly at low levels.

¹ Hardy, 1920.

2. Many communities of smaller plants are described which are stages in the development of the climax.

3. On the plateau under conditions of increased rainfall and humidity a heath-like type of vegetation is developed. The soil contains much humus. The climax is a community of bushes mainly of ericoid habit but containing also larger plants with broader leaves, chiefly *Leucadendron*. The developmental stages of this are described, both those following destruction and some of those colonising new soil.

4. In kloofs and other very sheltered parts forests are present. The trees are evergreen with polished elliptical leaves. The forests show decidedly hygrophytic characters in the presence of lianes, epiphytes, and abundance of ferns. Succession stages leading to forest are composed of shrubs with flat leaves much less xerophytic than the sclerophyll type.

5. On the cliffs there occur plant groupings that represent phases of development of these three types, together with some chomophytic and succulent plants.

6. All over the vegetation has been often destroyed by fire. Many of the resulting communities and successions are described.

7. The three main types of vegetation are briefly considered in regard to their relations to one another and to the vegetation of other regions.

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THE PLANT COLONISATION OF MERSE LANDS IN THE ESTUARY OF THE RIVER NITH

By W. L. MORSS.

(With 2 Maps and 8 Figures in the Text.)

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INTRODUCTION.

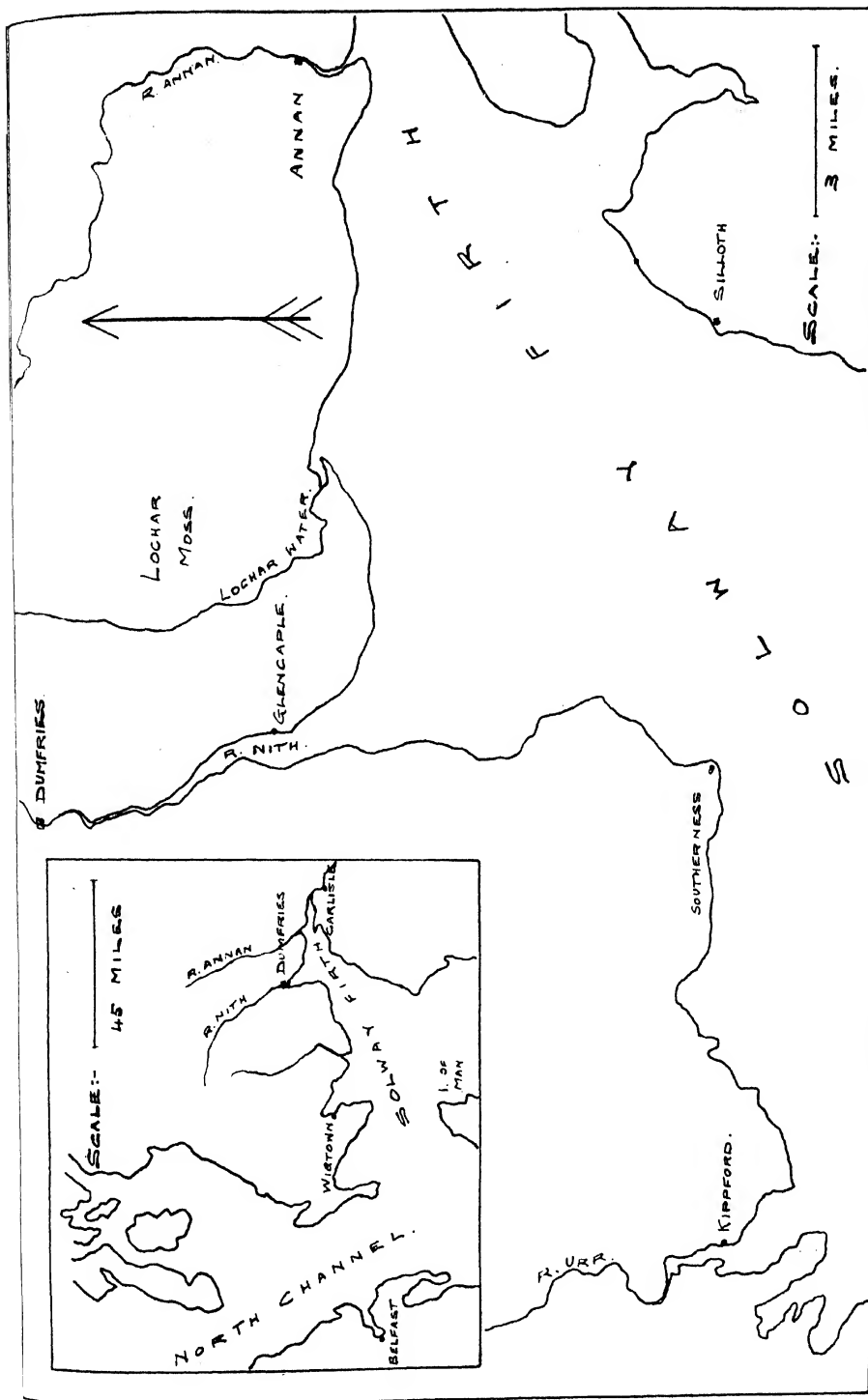
The term "merse lands" or simply "merse" is usually applied, in Scotland, to what are known generally south of the Tweed as "salt marshes" or "saltings." The word "merse" seems to have the same derivation as "marsh" (A.S. merse for mer-isc, i.e. mere-ish or full of meres). In Berwickshire "merse" is a corruption of "march" or boundary, and in some parts of Dumfriesshire it is used for alluvial land along a river.

The marshes under observation for the present work lie at the mouth of the River Nith, which forms, in its lower reaches, the boundary between Dumfriesshire and Kirkcudbrightshire.

The River Nith is tidal as far inland as Dumfries, which is about seven miles from Aird's Point on the right bank of the river, and about the same distance from Scar Point on the left bank, where the spring tide high-water mark bends away to the east.

The area of the merse lands up to this point in the estuary is approximately three square miles.

The merse lands on the right bank of the river terminate riverwards in an abrupt escarpment from one to three feet high over mud slopes that dip more or less gently to the low-water channel of the river. Beyond Aird's Point and



MAP 1. Sketch-map of part of the Solway Firth showing the relative position of the River Nith and its estuary.
Inset map of the south-western extremity of Scotland.

Scar Point, the estuary widens out to the Solway, but there is a deep low-water channel that at first hugs the western shore. On the Glencaple side there is a stretch of merse that gradually merges into naked flats of mud and sand which are exposed at low tide. Owing probably to the channel lying obliquely to those mud flats, the flood rushes up the river with a bore, the front wave of which may be several feet high. As a result, the loose mud is churned up by every tide and the water that inundates the merse always contains much mud in suspension. Consequently the merse must be continually increasing in height. That the siltings may be rapid in favourable circumstances is shown near Kirkconnell where mooring bollards are seen along what ninety years ago was a navigable channel, but is now firm grass land almost at the same level as the old bank.

In the upper estuary the current is too strong and the present channel too narrow and wanting in backwaters to permit of the emergence of new land. Erosion of the banks is taking place at some points.

The boundary of the merse away from the river is almost always sharply defined by a steep bank at the edge of the old 25-foot beach which forms an extensive flat terrace. Part of the 25-foot terrace is peat moss, some of which has been reclaimed and bears heavy crops. The merse itself, though frequently under water, is not a bog, but is moderately firm ground, through which numerous creeks meander. It is covered with nutritious herbage which supports a considerable population of cattle and sheep. Cattle that have not thriven on inland pastures are found to gain tone and fatten when transferred to the merse, probably owing to the salt (or mud) or to the vitamin content of the plants. Sheep with a tendency to consumption gain strength to a marked degree when put out for a time to graze on the merse¹.

Farmers are generally of the opinion that *Glyceria* is the chief plant eaten by the animals, but the result of observation of the sward of the plots throughout the season would seem to point to the fact that the stems and leaves of plants other than *Glyceria* are also eaten—particularly perhaps *Armeria*². It is practically certain from close observation that neither cattle nor sheep eat the flowers of this plant.

OBJECT OF THE RESEARCH AND SCHEME OF THE WORK DONE.

The object of this research was to ascertain the succession of plants that had colonised the mud flats and gradually converted them into merse, and also to study the conditions under which the merse plants grow.

For this purpose strips of ground traversing the merse from the mud slopes to the bank of the 25-foot beach were examined botanically. The flora was found to be fairly uniform, so that it was difficult to suggest a definite succession in the occupation of the ground.

¹ I am indebted for this information to Mr D. T. Blackstock, Flatts, Dumfries.

² Yapp (17), 5, p. 97.

An attempt to reproduce original conditions by removing the top spit of vegetation in one case, and all the soil in another, was abandoned. It was thought that the plants that appeared on the bare patches might indicate the earliest colonists, but the plants that grew up were seedlings of the plants surrounding the patches.

Except on the steep mud slopes, a census of plants did not show a great variation in the number per unit area but there was a marked difference in the size and vigour of the plants in different plots which seemed to point to the better adaptation of some plants to the prevailing conditions. The most easily applied criterion of the relative vigour of the plants seemed to be the length of their roots. Owing to some of the plants being cropped short by cattle and sheep the length of the stems would not have been a fair test. Hence a large part of this paper is concerned with the measurement of roots. The conditions governing the growth of the plants seemed to be mainly the amount of salt in the soil and its texture¹.

As a check on the observations of growth of plants in relation to amount of salt present in the soil, specimens of merse plants were grown in the mud in plant pots and watered regularly by solutions of Tidman's sea-salt of gradually increasing strengths. By this means the amount of salt the plants could stand was ascertained.

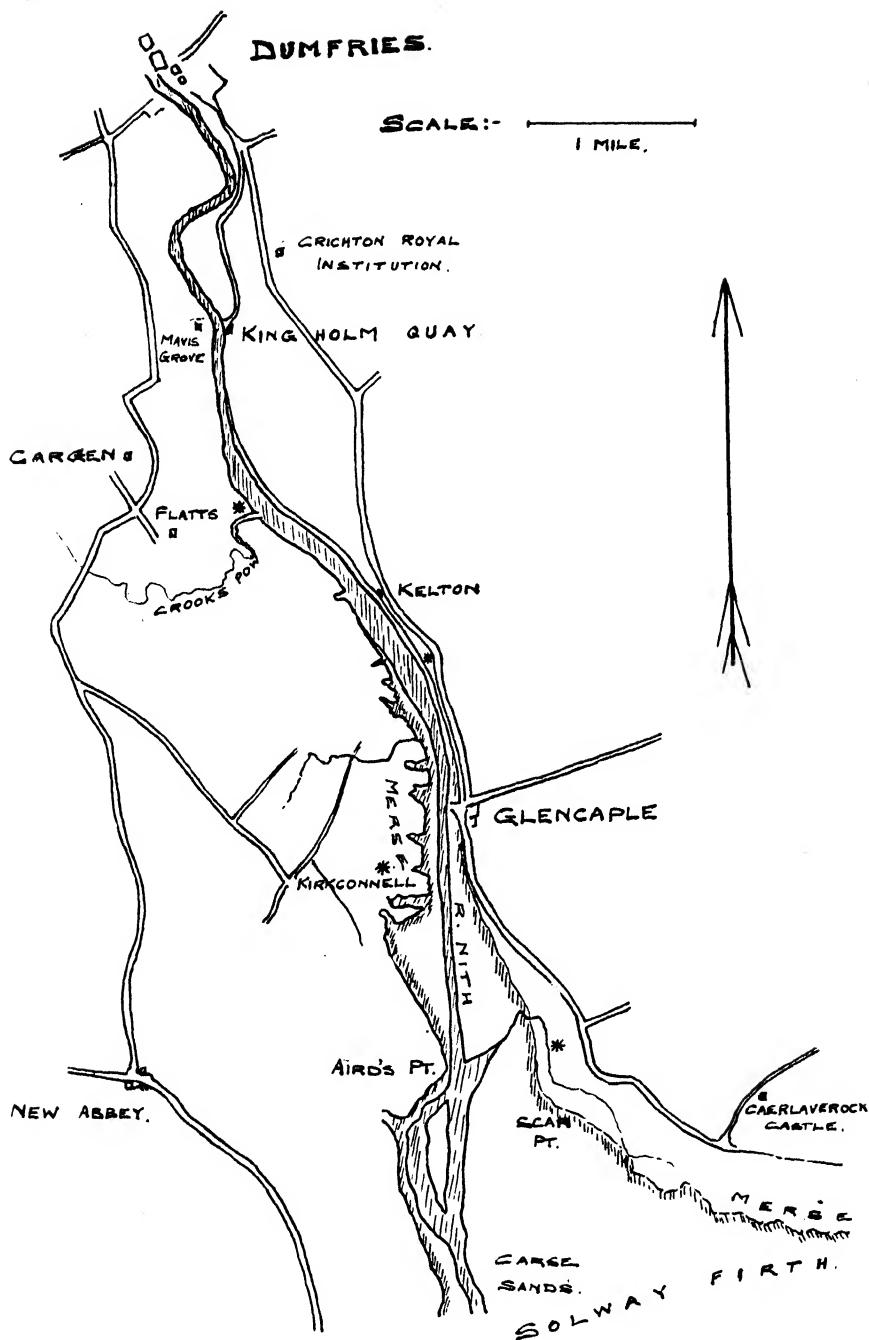
Four strips of ground, two on each side of the river, were selected; one where the estuary begins to widen out; the others farther up stream. These strips (whose positions are shown on the accompanying map) seemed to be fairly typical pieces of merse. Each traverse was divided into a number of plots in each of which the conditions were nearly uniform.

Observations were taken regularly from the middle of March to the end of September, 1923. At least one visit to the marshes was made per week, so that each section was seen at least once every three weeks. Consequently the succession of plants and their period of flowering were under observation throughout the season.

A plan and section of each traverse accompany a table showing the lengths of the roots of named plants on each plot and the percentage of salt in the dried soil of each plot.

Accompanying the appropriate table is a detailed description of the traverse with its complement of plots and a comparison has been made between the vegetation of the four areas and also between this vegetation and that reported by other workers on this subject.

In the spring of 1925 the acidity of the soil was studied, and the question of its aeration was investigated.



MAP 2. Map of part of the Nith Estuary. The positions of the traverses of merse land described in this work are shown thus *.

DETAILED DESCRIPTION OF THE AREAS STUDIED.

KIRKCONNELL.

Kirkconnell is situated about a mile north of Aird's Point mentioned in the introduction.

The largest stretch of merse land on the right bank of the Nith Estuary is found here. A section taken from Kirkconnell in line with Glencaple on the opposite bank is almost three-quarters of a mile in length. From this point northwards the merse gradually gets narrower.

The traverse at this place commences at the low-water level with a stretch of bare mud gently sloping inland for a distance of about seventy yards. Following this is a belt of about ten yards where the mud is occupied by small patches of *Glyceria*. Mingled with the stems and leaves of this plant are often found decayed leaves of deciduous trees such as oak, beech and wych elm, pieces of stems of grasses, rushes and other Phanerogams, and fragments of various species of brown and green algae, e.g. species of *Fucus*, also *Ulva lactuca*, *Enteromorpha compressa* and *E. intestinalis*¹. This belt constitutes Plot 1. Most tides cover it.

Plot 2 is in the same plane as Plot 1, but is quite distinct from it because of its uniform vegetation of which *Glyceria* is dominant. Isolated plants of *Armeria*, *Glaux*, *Plantago*, and *Spergularia* may be found. The general appearance of the plot is that of a newly sown lawn which is probably due, to a certain extent, to the daily cropping by cattle and sheep.

Now comes an abrupt line of demarcation in the form of an escarpment, eighteen inches high, where the established merse may be said to commence. The escarpment is the edge of a fairly level stretch of land extending inland for over a quarter of a mile. This is:

Plot 3. It is like an immense lawn and is more thickly carpeted than Plot 2. The vegetation is very uniform across the whole stretch, the only variations which occur being hollows (pans) of bare mud² and small areas slightly lower than the surrounding ground which are occupied by a higher percentage of *Glaux* plants³. Where there are irregularities at all in the surface *Glyceria* and *Armeria* predominate on the higher parts, and *Glaux* in the lower. This plot is cut up by many creeks which are filled to varying heights by the different tides. During spring tides they are practically filled to the level of the surrounding ground and water runs on to the more low-lying parts of the plot. When high spring tides prevail, most of this stretch is submerged.

Plantago may be found in places, particularly where the ground is wet. Specimens of *Cochlearia* are scarce except in the soft mud of the creeks where it is found in abundance, but it apparently does not favour the more open parts of the creeks near the sea.

¹ Oliver (8), p. 13. Walton (15), p. 115.

² Marsh (7), p. 84.

³ Yapp (17), p. 95.

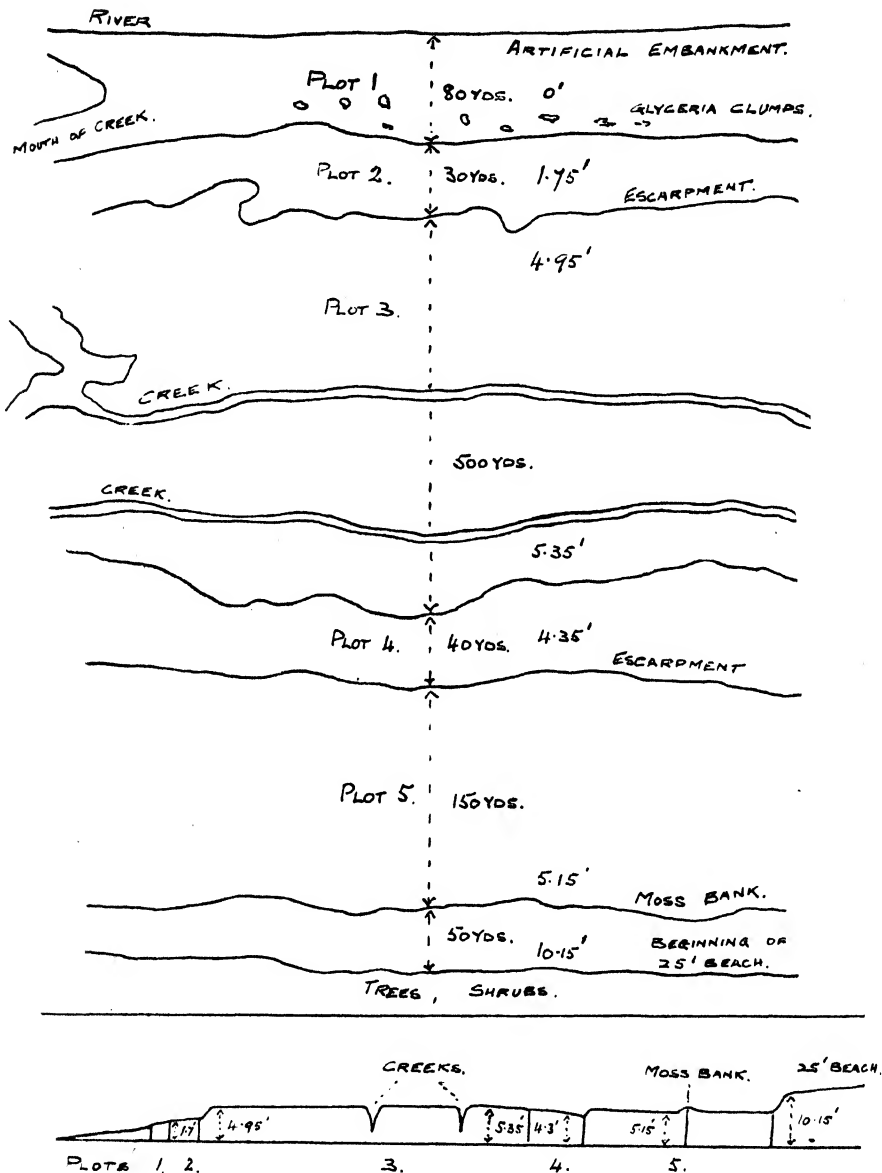


FIG. 1. Plan and section (not drawn to scale) of the traverse of merse land at Kirkconnell. Heights are shown in feet above datum. For detailed description see text.

Plot	PLOT 1.	PLOT 2.	PLOT 3.	PLOT 4.	PLOT 5.	MOSS BANK.	EDGE OF 25M. BEACH.
SALT MARSH	GLYCERIA MARITIMA. 10	GLYCERIA MARITIMA. 10 ARMERIA MARITIMA. 8. GLAUX MARITIMA. 14½ PLANTAGO MARITIMA. 7. SPERGULARIA MARINA. 15.	GLYCERIA. 15. ARMERIA. 18. GLAUX. 4. PLANTAGO. 12.	GLYCERIA. 15. ARMERIA 3½. PLANTAGO. 7. SPERGULARIA. 14½. ASTER TRIPOLIUM. 4½. SALICORNIA HERACEA. 2. TRIGLOCHIN MARITIMUM. 5.	GLYCERIA AND OTHER GRASSES. 24. JUNCUS COMPRESSUS. 24. ARMERIA. 7. PLANTAGO. 8. LEONTODON AUTUMNALIS. 3. GLAUX. 2½. TRIGLOCHIN (IN CREEK. SALT = .53%)	BELLIS PERENNIS LOTUS CORNICULATUS.	HOLCUS LANATUS. LOLIUM PERENNE. RANUNCULUS ACRIS. LOTUS CORNICULATUS. CERASTIUM VULGATUM. CARDUUS ARVENSIS. ULEX EUROPAEUS.
	MUD LOOSE AND LIGHT-COLOURED.	MUD AS IN PLOT 1.	MUD FIRMER THAN IN PLOTS 1 AND 2, BUT ON DRYING BREAKS UP INTO A FINE TILTH.	MUD SODDEN, STICKY AND MORE OR LESS CLAYEY; DRIES HARD; DARK.	MUD APPROACHES ORDINARY EARTH IN COLOUR AND TEXTURE.	MUD BREAKS UP FINE; SLIGHTLY SANDY.	SOIL - FINE.
	SALT .33%	SALT .38%	SALT .26%	SALT 1.33%	SALT .13%	SALT .07%	SALT .067%

FIG. 2. Table showing the species occurring on the Kirkconnell traverse. The salt percentages given represent grams of salt (sodium chloride) per 100 grams of dried mud. The figures following names of species represent average depths of roots in inches.

Cattle and sheep when turned on to the merse between the high tides seem to seek this plot in preference to any other.

Plot 4 is lower than Plot 3, and is in the form of a shallow channel, running parallel to the river¹. It is covered by spring tides which sweep along it, cutting off almost the whole merse and leaving a good deal of Plot 3 practically dry, except at high spring tides.

The soil is always wet and sticky and the vegetation sparse compared with the plots on each side of it. This will partly account for the great difference in the amount of salt present in Plots 3 and 4. The high percentage of salt and the stickiness of the mud may be due to the fineness of the grains resulting in greater retention of water and in greater absorption of salt.

Aster, *Spergularia*, *Salicornia*, *Triglochin* and *Cochlearia* flourish, but specimens of *Armeria* are poor and few.

An escarpment eighteen inches high separates Plot 4 from Plot 5.

Plot 5. This is only covered by high spring tides. Compared with the foregoing plots, it is much more thickly clothed with vegetation. The appearance of such plants as *Leontodon*, *Juncus* and grasses other than *Glyceria* amongst some of the more typical marsh plants already discussed, give this plot the appearance of purely inland sward².

It is very similar to Plot 4, Crooks Pow, and to Plot 3, North Glencaple, but has not the variety of plants to be found on the latter plot. The presence of *Lotus corniculatus* and *Trifolium repens*, for instance, on Plot 3, North Glencaple, suggests that this plot is older merse than Plot 5 at Kirkconnell.

The roots of *Armeria*, *Plantago* and *Glaux* which gradually get shorter as one moves away from the river, that is, as these plants are getting more choked out by other plants, are shorter in Plot 5, Kirkconnell, than in Plot 3, North Glencaple. This is the opposite to what one would expect, but is accounted for, I think, by the fact that the soil of the plot at Glencaple is softer than that of the plot at Kirkconnell. *Triglochin* is found on some of the lower parts of the plot.

It will be noticed from the table that the roots of *Glyceria* and other grasses penetrate deeply into the soil, whereas the roots of *Glaux* are very short. At this part of the merse *Glyceria* is well established, and as the salt percentage is getting less it approaches the form of ordinary meadow grasses. The sward is thick, and consequently *Glaux*, which likes a more open soil with more salt is practically choked out. It is quite choked out on the moss bank.

There is a sharp distinction between the sward of Plot 5 and that of the bank and also of the edge of the 25-foot beach. These two are seldom touched by tides and even then it is only the lower edge of the raised beach that gets any salt from the sea water.

The vegetation shows none of the characteristics of the merse. As already mentioned, a square yard of turf removed and the soil turned over, produced

¹ Priestley (11), p. 54.

² Warming (16), p. 231.

no seedlings of marsh plants during the summer of 1923. Only seedlings of plants growing on the surrounding raised beach were observed.

CROOKS POW.

Of the four traverses studied, this is the farthest up the estuary. The river here is confined to a comparatively narrow channel and even at high tides the area of land submerged is small compared with that at Kirkconnell. The actual amount of merse land is much less than at Kirkconnell.

The whole merse is covered by high spring tides which reach up to the bank shown in the sketch.

Crooks Pow is a fresh-water stream which always brings down a much larger volume of water than any of the large creeks which cut their way through the merse at Kirkconnell.

Plot 1 on this section consists of a steep slope of mud stretching inland from the low-water mark. The surface mud is soft and this lies on a bed of firm blue mud. Isolated plants and also clumps of *Glyceria* have established themselves on the landward edge of this plot.

Plot 2 lies on the same incline as Plot 1, but luxuriant plants of *Glyceria* have spread themselves out into a uniform patch. A few plants of *Aster*, *Glaux* and *Cochlearia* appear here and there and particularly fine specimens of these are found on a flat strip about a yard wide adjoining Plot 3, the edge of which is an escarpment three feet high which separates it from Plot 2. Brine is constantly dripping down the face of this escarpment. Soil also falls occasionally on to the strip owing to the crumbling away of the bank. These two factors most probably account for the luxuriance of *Aster* and its companions.

Plot 3 is fairly level and is terminated abruptly on one side by the steep banks of Crooks Pow. At Kirkconnell there is no part of the merse quite like this plot. The vegetation is more luxuriant and the soil is usually wetter than on areas producing the same kinds of plants at Kirkconnell.

A point worth noting is that the roots of *Glaux* are longer than those of Plot 3 at Kirkconnell. *Cochlearia* is plentiful everywhere on the plot, whereas on the corresponding plot at Kirkconnell this plant is scarce except on the sides of the creeks. *Cochlearia* is particularly luxuriant in the narrow tributaries of the Pow.

Unlike all the plots at Kirkconnell and Plots 1 and 2 at this traverse, Plot 3 is not rectangular, but winds about the bases of two other higher patches which constitute Plot 4.

The plan shows the position of the two patches forming Plot 4, standing higher than the surrounding ground and supporting such plants as *Leontodon* and *Plantago coronopus*. A portion of the turf (about twelve square yards) was removed two years ago for the purpose of repairing lawns and on the bare soil which was exposed specimens of *Armeria*, *Plantago*, *Maritima* and *Glaux* are now appearing.

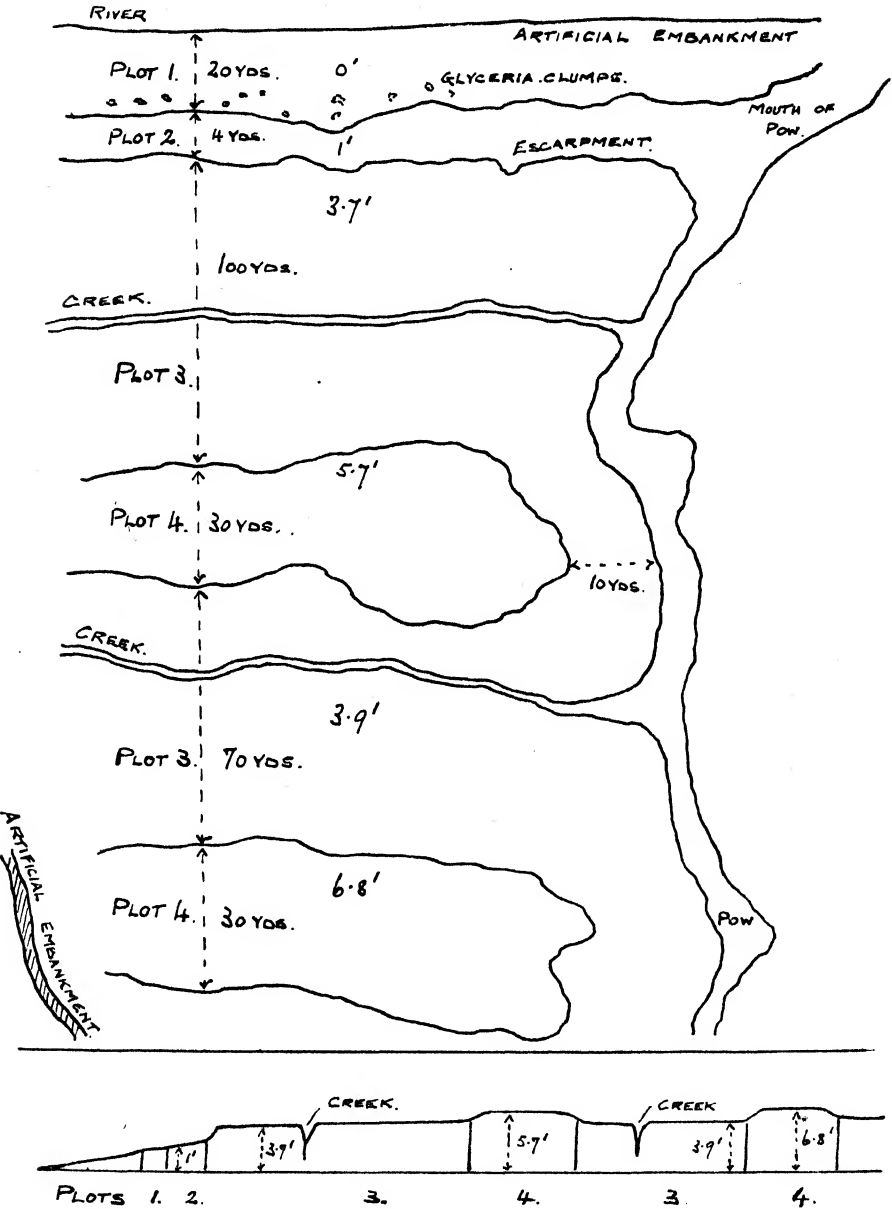


FIG. 3 Plan and section (not drawn to scale) of the traverse at Crooks Pow.
Heights are shown in feet above datum.

An interesting fact here is that the salt percentage is higher than in the lower surrounding Plot 3. The salt percentages found in the soil of all the plots of this traverse are low, especially in Plots 1 and 2. This is discussed under the heading of salt percentages, in the conclusions.

PLOT	PLOT 1	PLOT 2.	PLOT 3.	PLOT 4.	CREEK.
SPECIES	GLYCERIA MARITIMA. 6.	GLYCERIA MARITIMA. 17. ARMERIA MARITIMA. 11½. GLAUX MARITIMA 5¾. PLANTAGO MARITIMA. 9. COCHLEARIA OFFICINALIS. 4¾. ASTER TRIPOLIUM. 6½.	GLYCERIA. 15. ARMERIA. 22. GLAUX. 6¼. PLANTAGO. 25. COCHLEARIA. 4. ASTER. 7.	GLYCERIA AND OTHER GRASSES. 20 ARMERIA 10. GLAUX. 2. PLANTAGO CORONOPUS. 10. LEONTODON AUTUMNALIS 4.	ASTER 7 COCHLEARIA. 7.
SOIL	MUD IS LIGHT BROWN, 4" DEEP, COVERING FIRM BLUE MUD. DRIED MUD BREAKS UP FINE.	BROWN MUD OVER BLUE MUD. DRIES HARDER THAN THAT OF PLOT 1.	MUD IS VERY FIRM.	MUD DRIES VERY HARD.	MUD DRIES FAIRLY HARD.
SALT	SALT .08%.	SALT .09%.	SALT .11%.	SALT .14%.	SALT .11%.

FIG. 4. Table showing the species occurring on the Crooks Pow traverse. Figures showing salt percentages and depths of roots are as explained in the legend to Fig. 2.

SOUTH GLENCAPLE.

The merse land under observation at South Glencaple is on the left bank of the river and the traverse selected for detailed study is about a mile and a half south of the village of Glencaple. In this part of the river estuary the roadway for a considerable distance runs close alongside the merse, being separated from it only by a hedgerow and a narrow belt of rushes and gorse bushes with a few scattered trees. The highest tides flood the rushes and reach up to the trees and bushes.

The length of the traverse from the river to the belt of trees is about a quarter of a mile. From this point the marshes bend away eastward round Scar Point to the open Solway, extending to a distance of several miles and broadening out until, in some parts of the Caerlaverock district, the flats are clothed with typical merse flora for a breadth of over a mile.

The general condition of the vegetation along the traverse at South Glencaple gives one the impression that this part of the merse is much younger than those already described at Kirkconnell and Crooks Pow. The sward is much less dense and at no part does *Glyceria* present the lawn-like surface which

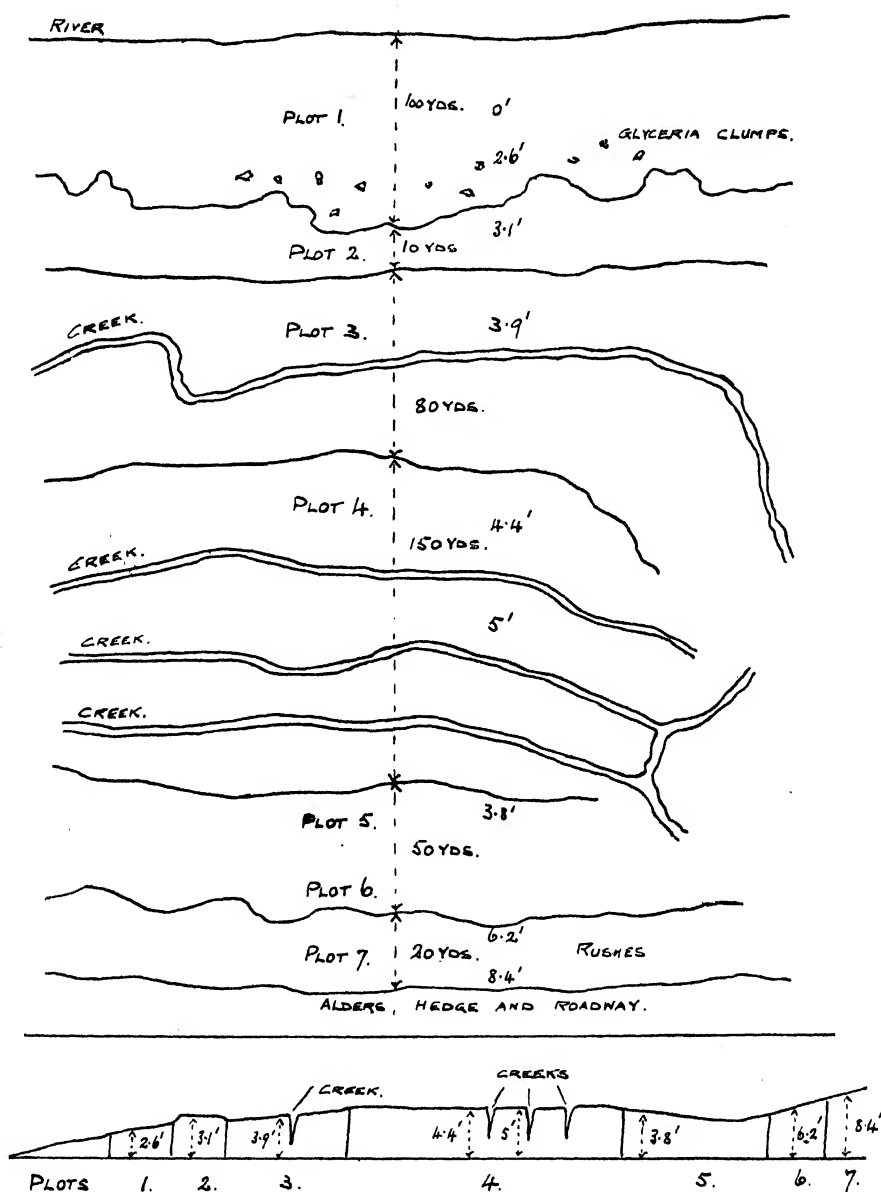


FIG. 5. Plan and section (not drawn to scale) of the traverse at South Glencaple.
Heights are shown in feet above datum.

Plot 1.	Plot 2.	Plot 3.	Plot 4.	Plot 5.	Plot 6.	Plot 7.
GLYCERIA MARITIMA. 8. SALICORNIA HERBACEA 4 $\frac{1}{2}$.	GLYCERIA MARITIMA. 15. ARMERIA MARITIMA. 13. PLANTAGO MARITIMA. 24. SPERGLARIA MARINA. 12. ASTER 8 $\frac{1}{2}$. TRIPOLIUM. 8 $\frac{1}{2}$. COCHLEARIA OFFICINLIS. 4. SALICORNIA HERBACEA. 1 $\frac{3}{4}$. SUAEDA MARITIMA. 3.	GLYCERIA. 18. ARMERIA. 9. GLAUX MARITIMA. 9. ASTER. 9. SALICORNIA 2 $\frac{1}{2}$. SUAEDA. 3.	GLYCERIA. 22 $\frac{1}{2}$. ARMERIA. 9 $\frac{3}{4}$. GLAUX. 6. PLANTAGO. 13 $\frac{1}{2}$. SPERGLARIA. (ON EDGE OF A DEEP POOL) 17. ASTER. 4. COCHLEARIA. 3 $\frac{3}{4}$. SALICORNIA. (IN A HOLLOW) 6.	TRIGLOCHIN MARITIMUM. 5 $\frac{1}{2}$. PLANTAGO 9.	PLANTS AS IN PLOT 5.	JUNCUS MARITIMUS. J. ARTICULATUS - LAMPPOCARPUS. J. COMPRESSUS. J. COMMUNIS. RANUNCULUS FLAMMULA. SAMOLUS VALERANDI PHRAGMITES COMMUNIS CENANTHE LACHENALII
MUD IS LOOSE AND LIGHT-COLOURED.	MUD IS LOOSE.	MUD IS LIKE THAT OF PLOTS 1 AND 2.	MUD IS FIRM.	THIS PLOT IS VERY WET AND THE MUD IS VERY STICKY; DRIES HARDER THAN THAT OF PLOT 4	SOIL DRIES VERY HARD. THE PLOT IS WATER-LOGGED.	SOIL IS GRITTY.
SALT a. .24% b. .42%	SALT a. .27% b. .33%	SALT a. .23% b. .39%	SALT a. .59% b. .54%	SALT a. .55% b. .77%	SALT a. .124% b. .93%	SALT a. — b. .12%

FIG. 6. Table showing the species occurring on the South Glencaple traverse. Figures showing salt percentages and depths of root are explained in the legend to Fig. 2 and in the text.

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obtains in great stretches on the Kirkconnell merse. There is no patch corresponding to Plot 5 at Kirkconnell or Plot 4 at Crooks Pow and the soil is generally wetter than at these places, especially on low-lying places near the rushes.

The plots at Kirkconnell are in distinct terraces but here there is no clear line of demarcation between the plots except the bank which separates Plot 1 from Plot 2.

The pioneers here are *Glyceria* plants as at Kirkconnell and Crooks Pow. A few yards farther inland specimens of *Salicornia* appear and as the distance from the river increases these plants become more numerous. As at the preceding traverses, *Glyceria* tends to grow in clumps. This stretch of thinly clothed mud constitutes Plot 1.

Separated from this by an irregular escarpment about a foot high is Plot 2 which is a narrow strip richly clothed with eight kinds of merse plants. The specimens are well developed but the sward is not dense¹.

Plot 3 is a few inches lower than the preceding one and winds about on each side of one of the main creeks. It is generally wetter than Plot 2 and supports fewer kinds of plants. The percentage of *Glyceria* plants is lower.

Slightly raised from this plot and irregular in outline is Plot 4, which is mainly distinguishable from the surrounding ground by the thick bed of plantains on the landward half of the plot. This is a very noticeable feature, as specimens of this plant are very scarce on Plot 3. The patch had a decided brown colour in September, owing to the great number of fruit stalks. This plot is not touched by neap tides but is covered by tides on each side of springs.

Plot 5 is lower than Plot 4 and the mud seems to retain a good deal of the brine from the higher tides. Some salt water also finds its way on to it from some of the smaller branches of creeks during neap tides. Owing to the sticky nature of the soil, it is very difficult to measure the depth of the roots. *Glyceria* is very thinly scattered. *Triglochin* is plentiful and luxuriant.

A waterlogged strip between Plot 5 and the bed of rushes is Plot 6. The vegetation here is similar to that of Plot 5, but, if anything, more sparse. As will be seen from the table the salt percentage is considerably higher, due no doubt to the low-lying position of the ground and to the finer texture of the soil.

From the edge of this boggy area the ground rises rapidly (1 in 5) to the road.

NORTH GLENCAPLE.

The fourth traverse is about a mile to the north of Glencaple. Here a hedge-row separates the merse from the highway. Unlike the merse at South Glencaple, this is in distinct terraces and somewhat similar to that at Kirkconnell.

The whole merse is covered by high spring tides.

The mud slope is fairly steep (gradient, 1 in 4). The first part of this slope is a terrace of soft mud and raised a few inches above this is a second terrace

¹ Plots 1 and 2 no longer exist, the river, since these observations were made, having swung much nearer the eastern shore and carried away large portions of the mud banks.

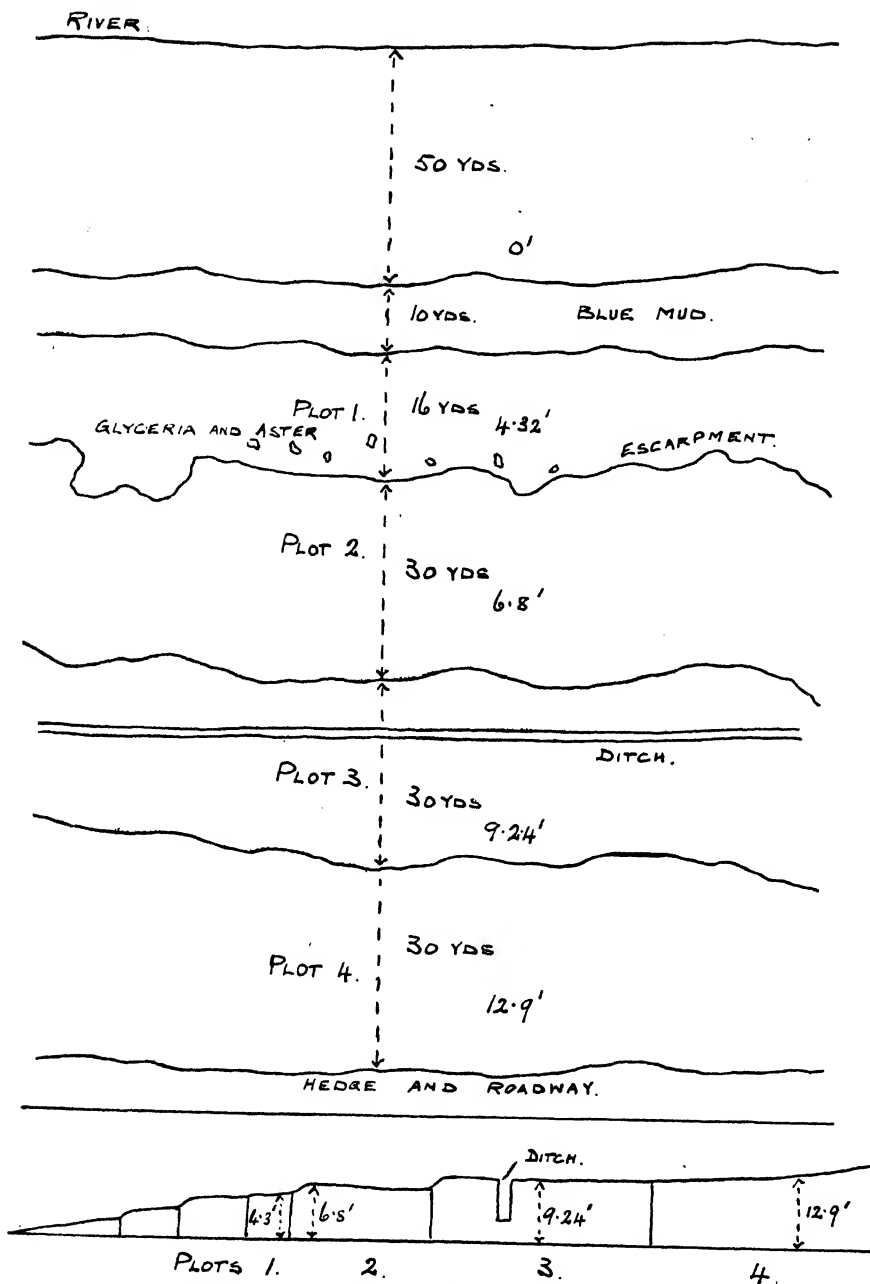


FIG. 7. Plan and section (not drawn to scale) of the traverse at North Glencaple.
Heights are shown in feet above datum.

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which is largely made up of a dark slatey blue mud which is much firmer than that of the first terrace. This blue mud exists on both sides of the river, at all four sections. There is a distinct stratum and the edge of terrace No. 2 here is an outcrop of it. The inference from this is, I think, that the blue layer is a "geological" stratum that extends under the whole merse. This stiff layer is overlaid by a more or less thick coating of brown mud of recent deposition through which the wayfarer sinks till he reaches the blue clay. If there happens to have been much wave action in some states of the tide, the loose mud may almost entirely disappear, while after prolonged calm weather one may sink over the gum-boots.

Plot	PLOT 1.	PLOT 2.	PLOT 3.	DITCH THROUGH PLOT 3.	PLOT 4
SPECIES.	<p>GLYCERIA MARITIMA 11</p> <p>ASTER TRIPOLIUM 5½</p>	<p>GLYCERIA 16.</p> <p>ARMERIA MARITIMA 11.</p> <p>GLAUX MARITIMA 7.</p> <p>PLANTAGO MARITIMA 9.</p> <p>SPERGULARIA MARINA 5.</p> <p>COCHLEARIA OFFICINALIS 4.</p> <p>TRIGLOCHIN MARITIMUM 8.</p> <p>SALICORNIA HERBACEA 2.</p>	<p>GLYCERIA 16.</p> <p>ARMERIA 23.</p> <p>GLAUX 4.</p> <p>PLANTAGO 19.</p> <p>LEONTODON AUTUMNALIS 2½</p> <p>PLANTAGO CORONOPUS 4.</p> <p>AGROPYRUM REPENS</p> <p>LOTUS CORNICULATUS</p> <p>TRIFOLIUM REPENS.</p>	<p>TRIGLOCHIN MARITIMUM.</p> <p>ASTER TRIPOLIUM</p> <p>ATRIPLEX PATULA</p>	<p>SCABIOSA SUCCISA</p> <p>CENTAUREA NIGRA</p> <p>POTENTILLA ANSERINA.</p> <p>RANUNCULUS AGRIS.</p> <p>CARDUS ARvensis</p> <p>HOLCUS LANATUS.</p> <p>AGROPYRUM REPENS.</p>
SOIL	MUD BREAKS UP ON DRYING.	MUD DRIES HARDER THAN THAT OF PLOT 1.	SOIL BREAKS UP ON DRYING.		SOIL LOOSE AND PURS.
SALT	SALT .53%.	SALT .56%.	SALT .07%.	SALT 4.21%	SALT .10%.

FIG. 8. Table showing the species which occur on the North Glencaple traverse. See legend to Fig. 2 for explanation of salt percentages and figures opposite names of species.

The soil on this terrace is pitted by innumerable tiny holes which are the burrowings of immense numbers of the amphipod *Cocophium longipes*, Linn. which can be found generally on the four traverses, but particularly on this terrace at this traverse. These crustaceans no doubt burrow through the loose brown mud to the stable foundation of blue mud, and it is possible that they help to fix the bottom of the brown mud by their exuviae¹. No doubt these animals play a great part in the aeration of the soil, taking the place of earth-worms.

Terrace No. 3 consists of a thicker layer of brown mud (about four inches) lying on the blue mud.

On the inner edge of this terrace *Glyceria maritima* appears in patches and after three or four yards has a good hold on the mud. The *Glyceria* clumps at

¹ Scott Elliot (12), p. 3.

this point are intermingled with specimens of *Aster tripolium*. This stretch of vegetation which is flooded by neap tides constitutes *Plot 1*.

The next terrace is occupied by *Plot 2*, which is raised above the preceding plot about twelve inches.

Glyceria, which is fairly well established, is mixed with numerous other kinds of salt-marsh plants, making the plot very like *Plot 2* at South Glencaple. The sward may, however, be denser. The landward edge of the plot is wetter than the seaward edge and the plants are more thinly scattered. *Triglochin* and *Salicornia* grow here.

Plot 3, which is from twelve to sixteen inches higher than the more seaward plot, is covered only by high spring tides, and is interesting because of the comparatively low salt content of its soil. Cutting through the plot is a drainage ditch about two feet deep usually containing salt water. A sample of this water, on analysis, showed the high salt percentage of 4.2. *Atriplex patula* flourishes in it and *Triglochin* and *Aster* also appear.

Beyond *Plot 3* is a gentle slope which is distinguished from the rest of the merse by its thick sward which shows little of the general character of merse land; this is *Plot 4*. A few stunted specimens of *Armeria* may be found, but with this exception the plants are those which are usually to be found in a settled land flora. High spring tides reach up to the seaward edge of this plot.

COMPARISON OF THE VEGETATION ZONES AT THE FOUR TRAVERSES.

Unlike the salt marshes described by Oliver and Salisbury at Blakeney Point, the marshes at Kirkconnell, Crooks Pow, North Glencaple and South Glencaple seem to show a similarity in the series of stages of colonisation from the bare mud alongside the river to the settled land flora on the landward side of the merse. *Plot 1* at each of the four sections composes the first of these stages, viz. *Zone 1*.

The salt marshes at Blakeney consist of "a whole series of small isolated marshes in different stages of colonisation." The parts showing the earliest stages of colonisation "consist of a sparse scattering of *Salicornias* in very open formation, the only other plants being Algae such as *Rhizoclonium*, *Chaetomorpha*, and *Enteromorpha*."

This agrees with the process at South Glencaple with regard to *Salicornia*, but *Glyceria* is present, also sparsely scattered, and Algae are present, chiefly *Enteromorpha*. The presence of *Glyceria* agrees with the vegetation of *Zone 1* of *Pool III* in the Spitzbergen salt marsh, described by Mr Walton. *Glyceria vilifolia* occurs there. Prof. Yapp says that *Salicornia* plays but a subordinate part in the building of permanent marsh in the Dovey Estuary—the earliest coloniser is *Glyceria*.

At Holme-next-the-Sea, Marsh says that *Glyceria* "appears in the very earliest stages, and gains its importance—from its perennial stoloniferous

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habit." This is also the case in the Nith Estuary. The only other plants in this zone at Holme are *Rhizoclonium* and *Enteromorpha* which form the substratum on which *Salicornia* seedlings germinate.

In several places at South Glencaple, *Glyceria* is distinctly the pioneer, although at others *Salicornia* is to the forefront. At the other three traverses *Salicornia* is absent in this zone; *Glyceria* is alone, except at North Glencaple where the plants are intermingled with specimens of *Aster*. The vegetation is "open" in all cases.

At the next stage the vegetation is "closed" at all the four stations. Plot 2 at Kirkconnell, Crooks Pow, North Glencaple and Plots 2 and 3 at South Glencaple show similar characteristics and consequently are studied together under Zone 2. At each traverse, *Glyceria* plants are more uniformly scattered and the percentage number per unit area appears to be considerably higher than on Zone 1. This is no doubt partly due to the rapid spreading by stolons. At the two western traverses the vegetation seems to be of a similar nature and differs somewhat from that of the two on the other side of the river. There is the same admixture of scattered specimens of *Armeria*, *Plantago*, *Spergularia*, and *Glaux*, but at Crooks Pow *Aster* and *Cochlearia* appear and *Glyceria* is more luxuriant.

On the eastern side of the river the corresponding areas forming this zone are much alike. There is a greater variety of plants than on the western side; *Salicornia* and *Suaeda* are both present, and *Triglochin* appears at North Glencaple. *Salicornia*, however, is not so vigorous, that is, the plants are smaller than in the open formation of Zone 1.

Glyceria is not so much in evidence on this side of the river, consequently there is not the same lawn-like appearance of the sward.

This zone¹, at the two Glencaple traverses, seems to correspond to the second stage at Blakeney Point, where there is the same close formation of *Salicornia* and *Glyceria*, but with this difference, that the *Statice Limonium* and *S. Humilis* of Blakeney are absent. *Statice* is plentiful on the merse at Kippford in the estuary of the Urr, the next estuary to the west of the Nith and still more plentiful in Orchardton Bay, farther west. *Statice Limonium* is recorded by Sutherland as occurring on the saltings north of Wigtown at the north-west of Wigtown Bay¹.

The general characteristics in the Nith Estuary closely follow the conditions in the *Glyceria-Aster-Statice* Society and the *Statice* Society at Holme-next-the-Sea. *S. Limonium* is the species found at Holme. In this society also occurs *Obione portulacoides*. This plant is quite absent on the four areas in the Nith Estuary². Prof. Yapp says that *Statice Limonium* and *Obione portulacoides* are completely absent on the Dovey marshes, and questions whether this is due to grazing or not. The Nith marshes support a great population of cattle

¹ Sutherland (13), p. 22.

² In April of this year (1927) a small patch was discovered by Dr Semple at Kippford.

and sheep and birds and this fact may account for the absence of these plants. On the other hand the Kippford merse is not so continuously used for grazing.

Another interesting point of difference is the absence of the carpet of Algae—*Pelvetia* and *Fucus*—which is a “marked feature” at Blakeney.

While Zone 1 on the Nith areas agrees closely with Zone 1 of Pool III at the Spitzbergen marsh, Zone 2 is unlike the corresponding stage there by the entire absence of the mosses. They resemble each other to the extent that there is “a certain amount of stranded *Enteromorpha*.”

This zone does not seem to be quite so pure in the *Glycerietum maritimae* association in the Dovey Estuary, which is often nearly pure, having only dwarf, stunted *Salicornias* associated with the *Glyceria*.

The plots which seem to form Zone 3 at the four traverses are shown in the table. The zone generally consists of a denser sward than Zone 2, giving the appearance of meadowland, and where the herbage is closely cropped by cattle and sheep and geese presents a lawn-like surface. *Glyceria* has now obtained a firm hold on the soil, making the turf more difficult to cut. *Armeria*, *Plantago*, *Glauz* are well established, *Armeria* especially being in evidence. This zone is the “*Armerietum* association” of the Dovey Estuary and the “*Statice* Society” and the southern belt of the “*Armeria* Society” of Holme. Other plants, such as *Aster*, *Triglochin*, *Spergularia*, *Cochlearia*, *Salicornia*, and *Suaeda* occur according to the varying conditions of wetness, salt content and texture of the turf in the same zone.

Marsh includes these plants, with the addition of *Statice*, in the “*Statice* Society.” Apart from this list is the special flora of the banks of those channels and pools in which there is a tidal rise and fall of the water level. These are edged with *Obione portulacoides*.

Salicornia is not the commonest plant of the zone as at Blakeney, but where it does grow, in the lower lying places, it is dwarfed, thus agreeing with Prof. Oliver’s observations. *Statice Limonium* is absent, also *Obione*, as before stated. Otherwise the vegetation at this particular stage seems to tally with that at Blakeney. Oliver, however, does not mention *Suaeda* and *Cochlearia*.

The vegetation of Zone 3 does not seem to have any parallel with that of the corresponding zone at the Spitzbergen marsh, mosses, lichens and the Cyanophyceae have not been found at this stage on the Nith merse. Like the *Armerietum maritimae* association of the Dovey Estuary, which it seems to resemble closely, the zone passes, at higher levels, into Zone 4, the *Festucetum rubrae* Association of the Dovey.

Zone 4 is only covered by high spring tides. With the closer growth of grass (*Glyceria* is now giving place to *Festuca*) and the much scarcer appearance of *Armeria* and *Plantago maritima*, the merse at this stage approaches the more purely inland sward. It is characterised at Kirkeconnell, Plot 5, Crooks Pow, Plot 4, and North Glencaple, Plot 3, by the presence of *Leontodon autumnalis*; and *Plantago Coronopus* appears at the two latter places. *Lotus Corniculatus*

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is encroaching and at North Glencaple the sward is still further advanced by an intermixture of *Agropyrum repens* and *Trifolium repens*. *Juncus compressus* is found at Kirkconnell. Most of these plants, however, are absent at South Glencaple, the soil being occupied by various species of rushes, the most conspicuous being *Juncus maritimus* which occupies the lower part of Plot 7.

The roots of *Armeria*, *Plantago maritima* and *Glauz*, where these plants exist, are generally much shorter at this stage and consequently their sub-aerial organs are stunted compared with the corresponding parts of plants growing in the lower and more "open" zones.

Zone 4 seems to correspond, at Blakeney, to the portion of the older marshes which are for the most part a thick carpet of *Obione*—amongst which the only plant which appears to grow with success is *Glyceria maritima*. *Plantago* and *Aster* are also present, but scattered and of rather rare occurrence. At Holme, *Glyceria* is co-dominant and the "Armeria Society" at this stage is passing into the *Festuca-Juncus* Society dominated by *Festuca rubra* and *Juncus maritimus*, and is continuous with the *Armeria-Festuca* belt.

Zone 4 on the Spitzbergen marsh is a slope of shingle with *Saxifraga oppositifolia*, *Dryas octopetala* and *Stereo caulon paschale*.

In the Dovey Estuary *Festuca rubra* is generally dominant. In many parts of the area two subassociations or societies can be distinguished, i.e. the Lower Festucetum, with abundant *Armeria maritima* which is usually subdominant, and Upper Festucetum, with *Agrostis alba*, *Plantago Coronopus* and *Juncus Gerardi*. The last two are the most characteristic plants.

The highest zone, Zone 5, is reached only by the highest spring tides, and when it is covered, which is rarely, it is by high storm springs. The general characteristics of this belt are the same at all four traverses. The flora is essentially mixed, halophytic and non-halophytic growing side by side, but the number of non-halophytic species increases as the upper limit of the zone is reached. The parts of the merse in the Nith Estuary which form this zone are the landward edge of Plot 5 and the seaward edge of the 25-foot beach at Kirkconnell, the landward edge of Plot 4 at Crooks Pow, Plot 4 at North Glencaple and Plot 7 at South Glencaple. At the first three places the sward is similar to that of Zone 4 but the salt marsh plants are now practically choked out. Stunted specimens of *Armeria* may be found, here and there, and also very small, isolated plants of *Glauz*. The soil is loose and gritty and consequently quite different from the firm clayey mud of the lower zones. A great variety of non-halophytic plants is found except at Crooks Pow. Such plants as *Cerastium vulgatum*, *Carduus Arvensis* and *Holcus lanatus* at Kirkconnell, and *Scabiosa succisa*, *Centaurea nigra* and *Potentilla anserina* at North Glencaple, show the advanced nature of the sward at this stage. Non-halophytic plants at Crooks Pow are almost confined to *Lotus corniculatus* and *Trifolium repens*.

Juncus maritimus, which is plentiful at Holme, Blakeney and on the Dovey marshes is only represented at one of the traverses studied, viz. at South Glen-

caple. Associated with this species are *J. articulatus*—*lamprocarpus*, *J. compressus* and *J. communis*.

The seaward edge of this belt of rushes shelters quite a number of plants, some of them merse plants such as *Cochlearia*, *Plantago*, *Aster* and *Triglochin* which almost disappeared in the lower water-logged parts of the more seaward zone. Many of these are luxuriant specimens. An interesting parallel is described by Prof. Yapp—he says that some plants of the *Armerietum* and Lower *Festucetum* zones reappear, which are almost absent in the Upper *Festucetum*, e.g. *Spergularia*, *Aster*, *Triglochin*. These are “far more luxuriant than on the sward.”

In the *Juncus* association in the Blakeney Point area, *Juncus maritimus* is the dominant plant, “growing in a short turf of *Agrostis maritima* and *Carex arenaria*, the occasional species being *Cochlearia officinalis*, *Sagina maritima*, *Anagallis arvensis*, and *Sedum acre*.” In the *Festuca-Juncus* Society at Holme, “the *Festuca* and *Juncus* form a close covering consisting almost entirely of these two plants with a little *Cochlearia anglica* and some lingering plants of the *Armeria* society.”

Hence it seems that however the characteristics of the vegetation may vary in the early stages of colonisation in the British marshes, the final stage, that where the salt vegetation passes completely into the ordinary land vegetation, is practically the same.

The final stage on the Spitzbergen marsh seems to consist of a growth of *Carex salina*, *Juncus lighemis*, *Salix polaris* and *Nostoc*.

THE FAUNA OF THE MARSHES AND ITS EFFECT ON THE SOIL.

The table¹ on p. 332 shows the average number of birds seen daily on the merse at different places throughout the year.

It will be noticed that, during the winter months, the marshes are regularly inhabited by enormous numbers of birds. In March there is a slight falling off in the numbers except in the case of geese and ducks.

During the spring and summer the numbers of all species are much less than in winter, owing to emigration, June and July being the two months when the merse is most free from bird population.

Following are some extracts from Gladstone's *Birds of Dumfriesshire*² and *Notes on the birds of Dumfriesshire*³.

“The Solway Firth has been likened by H. A. Macpherson to ‘a great ornithological junction.’ This valley of the Nith is a very well defined ‘fly-line,’ up and down which the birds pass in a north and south direction, in their vernal and autumnal migration, respectively; their emigration flight being in a direction which would take them down channel midway between the Isle

¹ I am indebted, for this information, to Mr Jas. Wilson of Glencaple, who is a well-known authority on the bird life of the district.

² Gladstone (3).

³ *Ibid.* (4).

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of Man and the opposite headlands of England." "The other 'fly-line' is directly east or west according to season."

"The Solway Firth affords ideal winter quarters for all sorts of geese, and the nature of the shores renders them particularly safe. The banks of the estuaries of the Annan and Nith are at times crowded with geese" (p. 239).

"In the early part of October, 1881, a flock of Barnacle geese was estimated at 10,000" (p. 251).

Time	Place	Birds
From the beginning of October to the end of February	Kirkconnell	Grey geese, 2000 Ducks, 400-500 Peewits, 1000 Curlews, 200 Gulls, 200-300 Redshanks, 200 (scattered)
January and February	Glencaple and Caerlaverock	Barnacle geese, 3000 Duck and widgeon, 3000 Gulls, 10,000 ¹ Peewits, 150 Oyster catchers, 500 Redshanks, 200 Curlews, 200 Golden plovers, 100 Dunlin, 500
March	Kirkconnell	Cormorants, 100 Grey geese, 2000 ² Ducks, 400-500 Peewits, 500 Curlews, 100 Redshanks, 100 Gulls, 150
April	"	Geese, 2000 Gulls, 200 Curlews, 100 Other species, 100
May	"	All species including Sheldrake, 200
June		
First three weeks	"	As for May
4th week	"	Gulls, 200 Other species, 100
July		
1st and 2nd weeks	"	Gulls, 500
3rd and 4th weeks	"	Gulls, 100 Other species, 200
August	"	Gulls, 1000 Curlews, redshanks, etc., 500

¹ These are seen on their favourite roosting ground.

² In severe weather the roosting places of the geese are sometimes so thickly covered with droppings as to give the ground the appearance of a poultry run.

"In the winter of 1920-21, Grey Lag geese were more than usually numerous near Glencaple—on 22nd of January, 1921, I counted one lot of 410 and was told this did not represent one half of the 'stock'" (*Notes*, p. 78).

Lapwings collect into emigration flocks in the autumn. In October, 1900, "it was estimated that there were congregated at least 50,000 birds whose murmurings were audible three hundred yards away" (p. 372).

"In autumn the numbers of Oyster Catchers to be seen on our shores are prodigious" (p. 377).

"An enormous flock (of starlings) said to have been of many thousands was seen near Cowheath (Caerlaverock), on 7th March, 1914" (*Notes*, p. 54).

In addition to the birds the marshes support a considerable population of sheep and cattle; on the Kirkconnell merse alone about 60 cattle and from 250 to 300 sheep regularly feed during the spring, summer and early autumn months.

The excreta of these animals and birds no doubt plays a very important part in the fertilisation of the soil. Ammonia from the decomposition of the organic matter of the excreta will be effective in neutralising any humic acid that may be present in the soil. The droppings of fish-eating birds should contain much calcium phosphate and carbonate from the fish bones.

The carapaces of the crustaceans already mentioned as occurring in great numbers on the mud slopes would add lime to the soil.

Pans remaining unflooded for several days before and after a low neap tide have been seen to contain living mussels of good size attached to the turf at the edge; whelks of fair size; undersized living cockles and many smaller molluscs; small crabs; shrimps and other small crustaceans, also small living flounders. In summer there is an enormous destruction of these small animals after each spring tide when the pans dry up during neaps. Many of these creatures are, of course, eaten by birds. Hundreds of little dead crabs in their carapaces have been seen on the merse. An examination of a square inch of bare soil revealed about a dozen corpses or carapaces.

The remains of these creatures and the excreta of birds and cattle and sheep will assist in the consolidation of the soil.

AERATION OF THE SOIL.

On one occasion, during a visit to the merse at Mavis Grove, there was noticed a huge gurgitation of air bubbles issuing from a gravel bed that dips under the clay of the river bank. The bubbling noise could be heard yards away. The air had got into the porous gravel under the stratum of clay when the tide sank. The bubbling was still going on even an hour after the ebb had set in. It is a common occurrence to see air bubbles rising from the mud banks and sides of creeks but it is not so apparent on the merse proper. On another occasion at Kippford, in May, whilst rowing over the merse in about three feet of salt water which covered it during a spring tide, there were seen sporadic zones of bubbling, and when an oar was pushed into the soil great bursts of gas came up. This was quite different from the rise of marsh gas from swamps and also distinct from the bubbling which takes place whilst photosynthesis is more in evidence during the summer.

The natural conclusion from these observations is that, for the most part, the soil of the salt marshes is porous and this is borne out by actual observation especially during the digging operations when measuring the depths of the roots. When the tidal water sinks air is sucked into the pores and when

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the tide rises the used-up air bubbles up. Oxygen dissolved in the water will, of course, be as efficient for the purpose of aeration as oxygen in the air.

In some parts of shallow pools of Plot 3, Kirkconnell, the mud looked as if it had been pricked all over with darning needles and at the mouth of each minute opening was a silvery air bell. Air bells were also enclosed by a mossy growth of *Alga*.

As mentioned before, the crustacean *Cocophium longipes* burrows in immense numbers into the bare mud flats and slopes, but during the digging operations on the merse itself, that is on the parts which are clothed with vegetation, these animals were not to be found at all. Worms also seemed to be absent. Earthworms do not exist anywhere where submergence by salt water is liable to occur. A story is told locally of a big tide which covered the high merse near Southernness, about eight miles south of Kirkconnell. One observer states that the tide on this occasion was at least six feet higher than the highest ordinary spring tides. A young plantation was killed and earthworms came up in millions and died. Gulls fed for weeks on the carcasses.

On cutting down into the soil, spaces left by dead roots were exposed to view and these had not all been filled up by soil. The root stocks of plants like *Plantago maritima* and *Armeria* extended down to great depths. It could be seen that these plants had kept pace, in their upward growth, with sedimentation. When the old root stock dies the external rind persists, leaving an air space where the softer tissues have decayed. These old root stocks would serve as air channels. As in the case of the burrows of the crustaceans, the clay surrounding the roots is light red-brown in colour where the clay itself is blue-grey, thus showing that the living tissues send down oxygen. On a slope of the Kippford merse the tops of many of the burrows were sticking up, in some cases about half an inch, above the level of the mud. At first it seemed that the burrow had a domed cap, but examination with a lens showed a hole in the centre filled with grains of sand. Samples of these burrows cylinders that were lying in the mud were heated in the fire, but there was no smell of decomposed nitrogenous matter, so that the cylinders were evidently not strengthened by mucus as was supposed, but were probably consolidated by iron rust. This seemed to be borne out by the fact that the burrows were each surrounded by a dark red zone.

During digging operations into semi-dried pans networks of burrows of polychaete annelid worms have been found. These extended a short distance under the turf. In pans filled with water, and in creeks, worm casts and openings into burrows were plentiful. Some of the recent worm casts were blue in colour. The mud surrounding the burrows was light red-brown in colour—showing that the burrows acted as channels for oxygenated water. The sides of the burrows were firmer than the rest of the mud, which could be washed away from some of the larger burrows, leaving them as tubes. Further, dead stolons of *Glyceria* and roots of surrounding plants were found, forming a

network in the semi-dried pan, though there was no vegetation showing above the soil. In many cases the roots seemed to occupy old burrows—at least the containing tube looked too big for the root. The annelid burrows evidently persist for a time and act as air channels when a filled pan is occupied by plants. The roots themselves will keep the mud porous thereafter.

pH DETERMINATIONS.

The object of these determinations was to compare the soil of the salt marshes with that of adjoining areas of peat moss and to try to discover the effect of the salt water and the excreta of birds and animals on the nature of the soil with a view to determine the causes of inhibition of certain species of plants from certain zones of merse land.

It was thought that the droppings of the enormous number of birds which regularly feed on the marshes during the winter and to a certain extent during the summer must play an important part in changing the nature of the mud precipitated on the banks of the river. The multitudes of small crustaceans and worms which can be seen burrowing into the soil and the extensive bubbling of gases during the rise and fall of the tide also seemed to be important factors in aerating the soil, and thus differentiate a porous, well-clothed soil from a sodden one with sparse vegetation of a limited number of species.

Specimens of channel water, water of pans, ditches, etc., of soil from various plots of the traverses studied, and also from several areas not necessarily in these traverses, under different conditions of weather tide, etc., were taken for the pH determinations. All the specimens seemed typical of the different areas from which they were taken and of the varying conditions prevailing at the time of selecting the sample.

The B.D.H. Universal Indicator was used.

The results of a few of these determinations are recorded below:

	pH
Water (slightly salt) from Nith Channel at slack water	8.2
Water of pans (salt to very salt) from Plots 2, 4, 5, 6, South Glencaple	7.8-8.5
Brackish water from pool at North Glencaple	7.8
Very salt water from ditch at North Glencaple	8.5
Soil from Plots 2-7, South Glencaple	7.2-8.0
Soil from Plots 1-3, North Glencaple	7.6-7.8
Soil from the Kirkconnell plots	7.8-8.3
Soil from middle of merse at Mavis Grove	6.5
The same, but with liquid extract filtered	6.8
Soil from a peat-moss area in the neighbourhood of Dumfries	4.0
The same, with extract filtered	5.5-6.0
Fresh water from a stagnant pool in the same area	4.0
Water from a muddy ditch on the landward edge of Plot 5, Kirkconnell, where the soil is black and foul-smelling, but occasionally submerged by salt water	6.6

Speaking generally, the following observations and deductions may be made from the foregoing figures:

(1) The soil of the salt merse is on the alkali side of neutral and this is no doubt partly accounted for by the excreta of the large flocks of birds which frequent the whole merse. The merse is more of the nature of a fen than of an ordinary marsh, and the soil is quite unlike that of a peat moss. Prof. Osborn,

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of the University of Adelaide, writing on the vegetation in the Port Wakefield District, says that the soil acidity does not show any great variation, with the exception of the soil of the zone farthest inland from the sea. All the soils, with the exception of the latter, have an alkaline reaction approximating to that of sea water (pH 8.6). The zone specially mentioned, where there is a decrease in the amount of salts and lime, shows a pH value for the soil of 7.4—just on the alkaline side of neutrality.

(2) With stagnant fresh water the reaction is on the acid side of neutral.

(3) With fresh water where, as on the bank of the river, the water drains away quickly and sucks down oxygen, the reaction is slightly on the alkaline side of neutral.

(4) Where the merse is frequently submerged by salt water, the reaction is alkaline.

(5) Even where the merse is sometimes submerged by salt or brackish water, if drainage from the fields above soaks the soil with fresh water, if the water is stagnant, the soil black and oxygen is not soaked down, the reaction is acid.

(6) It would seem that acidity has not much to do with differences in the vigour of the same kind of plant; *Glyceria* is most luxuriant where acidity is 6.8, and also where the acidity value is 7.8.

That acidity has some bearing on the inhibition of the growth of different species may be concluded from the various results shown.

Following are a few extracts from a communication from Prof. W. R. G. Atkins of Dublin, found in *Nature*, 108, 80, which support these conclusions:

Armeria maritima tolerates, pH 6.8–8.2.
Gorse usually on acid soils, pH 5.4–6.8.
Typical sand dune plants, pH about 8.
Typical moorland plants, pH about 5.

In *Nature*, 108, 147, is a letter in answer to the above, from Norman N. Comber of Leeds University, stating that there are strong indications that pH of soils has a mediate and not a direct influence on the flora.

(7) The following observations by Prof. Atkins are also interesting for comparison with the foregoing results:

Open sea, Plymouth to Ushant, pH 8.14–8.27.
Open sea, Land's End to Bristol Channel, pH 8.14–8.18.
In Plymouth Sound, pH 8.10.

In rock pools with growing marine algae the acidity sank by 0.25, owing to disappearance of carbonic acid by photosynthesis.

(8) The pH values for specimens which were filtered show very noticeable differences from those of specimens which were allowed to settle. It would appear that the filter kept back some very fine substance that was strongly acid. It is probable that the unfiltered liquid is nearer to the correct acidity of the soil water, for the water in a stagnant pool and in a slowly running ditch both turned the indicator brightly red.

An attempt to reproduce artificially some of the conditions under which

the plants were growing was made by obtaining wedges of soil bearing specimens of vegetation and watering these in suitable receptacles. Specimens of acid soils watered for a month with normal saline solution seemed to have a tendency to become neutral, e.g. in one experiment the figures were pH 6.6 to 7.0. Simple aeration seemed to have some effect in making soils more alkaline, e.g. where the specimen was kept loose in a flower pot and watered with neutral water the value changed from 6.8 to 7.8. When air was partially excluded by having the turf in a jam pot filled up with water the acidity was increased, 6.5 to 5.5.

The addition of $NaCl$ to the water in extractions had an accelerating influence on the rate of sedimentation.

CONCLUSIONS.

A. SALT PERCENTAGE.

Salt percentage depends on:

(a) The height of the preceding tide at the time. This will be more in evidence on plots which are only covered by tides on each side of the spring tides but not by neaps. Compare samples taken for analysis at South Glencaple from Plots 4 and 6, which are both higher than the other plots (except 7) covered by neap tides.

Sample (a), Plot 4, was taken on Aug. 18th (moon 1st q. 19th), sample (a), Plot 6, was taken on Sep. 1st (moon last q. Sep. 3rd), that is, both samples were taken just after high tides. Samples (b) from both plots were taken on Sep. 22nd (moon full, Sep. 25th), i.e. after low tides.

Note spring and neap tides occur two days after the moon's phases. It will be seen that samples (a) are higher than (b).

(b) Rainfall¹. The amount of salt present in the soil due to the tides is greatly modified by the rainfall a short time before the samples were taken. Abundant rainfall will mean considerable leaching of the salt. More rain fell just before Aug. 18th (16th and 17th, 17.6 mm.) than before Sep. 1st (Aug. 30th and 31st, 13 mm.) and this no doubt accounts for the greater difference between samples (a) and (b), Plot 6, than between (a) and (b), Plot 4. The comparatively heavy rainfall two days before Sep. 1st (13 mm.) most probably causes the salt percentage of samples (a), Plots 1, 2, 3, 5, to be lower than those of samples (b) from the same plots taken on Sep. 22nd, which was preceded by two days' rainfall, amounting to 6.5 mm.

The samples from Crooks Pow show a strikingly lower salt percentage. They were taken on Aug. 28th, immediately after a considerable amount of rain which fell on the 22nd–27th (35.8 mm.). This rainfall no doubt partly accounts for the comparatively small amount of salt found in these samples.

(c) The height of the plot above the average height of the tides; for instance, a plot may not be touched by neap tides but covered by all springs;

¹ Tansley (14), p. 331.

another may only be covered by high spring tides. A plot covered only by spring tides would be expected to show a lower salt percentage than those covered by all tides. This is seen in Plots 3 and 5 at Kirkconnell, the soil of which is more salt than Plots 1 and 2. There may, however, be a double effect; ground in the proximity of creeks bringing down a considerable quantity of fresh water, submerged by springs will be bathed with water with a fairly high salt percentage, whereas those submerged at every tide will at neap tides be leached by fresh water. A case which probably illustrates this is Plot 4, Crooks Pow, which has the highest percentage of the traverse. This may also partly account for the higher percentage of Plot 4, South Glencaple, than of Plot 3, which, to a certain extent, surrounds it.

(d) The proximity of creeks and ditches. If the course of the creek or ditch be free, drainage of the plot near it will be accelerated with consequent reduction of salt percentage. The samples of Crooks Pow were taken alongside the creek which empties itself briskly into the river channel. This, then, appears to be another important cause of the low figures for Plots 1, 2 and 3 at this traverse.

As mentioned before, the amount of salt found in the soil of Plot 3, North Glencaple, is very low compared with that of Plots 1 and 2, and in all probability the reason for this is partly due to the presence of the drainage ditch which cuts through the plot. Although the water of the ditch has no perceptible current, it is not stagnant, and its average height compared with the height of the plot being considerable (about two feet lower) will tend to drain away quickly the salt water from the plot, rather than cause it to be water-logged with brine.

(e) The nature of the mud. At the four places studied in the estuary, the soil seemed to be very similar, and at each place there was a considerable variation in the texture of the soil—from close-grained bare mud to porous, more or less gritty soil found at high-water mark¹. Mud of a fine texture dries hard, retains more brine and in some places is water-logged, thus giving the highest salt percentages².

This difference in the texture of the mud may be put down as one of the reasons for the higher salt percentage of Plot 2 as compared with Plot 1 in any of the traverses where the soil is noted as being stiffer and drying harder.

Plot 4 at Kirkconnell and Plots 5 and 6 at South Glencaple are examples of a close sticky soil bearing a large quantity of salt.

(f) Whether clothed with vegetation or not. Vegetation retards the recession of the ebb tide by obstructing the passage of the water, and the water, adhering to the outside of the plant stems, gradually sinks down into the mud. This also partly accounts for the higher salt percentage of Plot 2 than of Plot 1, where there is usually a considerable difference in the number of plants per unit area.

¹ Osborn (9), p. 394.

² Hall (5), pp. 75–79.

(g) The inclination of the ground. The greater the slope the more rapidly will the salt water drain off. From flat ground the water recedes very slowly and consequently the soil has a better chance of absorbing the brine. The inclination of the ground in Plots 1 and 2 at Crooks Pow is noticeably greater than anywhere else in the four traverses. (Gradient, 1 in 1·5; vertical measurement in feet, horizontal in yards. Compare with gradients in corresponding plots at other traverses; Plots 1 and 2, Kirkconnell, 1 in 6. South Glencaple—Plot 1, 1 in 19; Plot 2, 1 in 100. North Glencaple—Plot 1, 1 in 4; Plot 2, 1 in 13.) This factor seems to be important in helping to bring about this low percentage of salt at this part of the merse.

(h) The distance from the open sea. The relative density of the salt water will naturally get less the farther one goes up the estuary. It will be seen from the map that the estuary has narrowed considerably at the point where Crooks Pow empties itself into it, and consequently it would be expected that the merse here would receive less salt generally than at the other three traverses. Here again is a factor which partly accounts for the low salt percentage found on the plots at Crooks Pow.

B. THE VEGETATION.

1. *Glyceria*. This plant is predominant on most parts of the marshes. It is the pioneer at all the four traverses studied¹. Isolated specimens advance many yards ahead of other species on to the mud slopes, and only at South Glencaple is there any attempt at rivalry. Here *Salicornia* intermingles with the *Glyceria* plants, but the latter is distinctly to the forefront.

As judged by the highest percentage of plants per unit area, *Glyceria* flourishes best at Plot 3, Kirkconnell; Plots 2 and 3, Crooks Pow; Plot 4, South Glencaple; and Plots 1 and 2, North Glencaple. As a general rule, the roots go deeper as the salinity of the soil increases, but it is thinly scattered in waterlogged plots, although in these the highest percentage of salt is found. This is probably due to the want of oxygen in the subsoil. *Glyceria*, grown in pots containing soil from the merse and watered with salt solution of gradually increasing strengths, was quite healthy when specimens of *Armeria*, *Glaux*, etc., were obviously dying. On the other hand, a few plants of *Glyceria* growing in a pot left out in the open and exposed to rainfall were excellent specimens. The nearest approaches to these pot-grown plants, in appearance, on the merse, are on Plot 2, Crooks Pow, and on the sides of creeks. Here the plants are young and are not cropped by cattle and sheep. The roots of the naturally grown plants cannot, of course, be compared with those of the pot-grown ones.

2. *Armeria*. In contrast to *Glyceria*, the roots of this plant seem to increase in depth with decreasing salt. This does not completely hold good, for on the higher parts of the *Leontodon* patches, *Armeria* plants are thinly scattered and

¹ Collins (2), p. 388.

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the roots are comparatively short, but there it would appear, a more robust rival chokes them out. *Armeria* fares badly in the lower lying, water-logged plots, with a high salt percentage. As mentioned above, *Armeria* will not stand the amount of salt that *Glyceria* will, and the pot specimens died when 4.42 per cent. of salt was present in the soil. Towards the end of June, when *Armeria* is in full bloom, the marshes give the appearance of immense carpets of a beautiful pink¹.

3. *Glaux*. *Glaux* seems to flourish best in soil with a fairly high salt percentage, but it would appear that almost as important factors are the texture of the soil and the amount of water present. Good specimens can often be found on open patches with a deep soft soil which is fairly wet. In a hollow in Plot 3, Crooks Pow, with salt percentage 0.07 and soft soil which dries fine, *Glaux* had roots 7 in. long. And on Plot 2, Kirkconnell, which consists of deep soft brown mud, a specimen was found with roots 14½ in. Like *Armeria*, *Glaux* is almost choked out in the *Leontodon* plot. Pot specimens continued to be healthy for some time after *Armeria* plants showed sign of uncomfortable conditions.

4. *Plantago*. Factors ruling the growth of *Armeria* seem to agree closely with those for *Plantago*, except that the latter seems to endure a wet soil better than *Armeria*. It may be found, in a healthy condition, in wet places with a fairly high salt percentage where *Armeria* would present a sorry appearance. *Plantago*, however, died in the plant pots when only 2.3 per cent. of salt was present. Hence, already, it must be concluded that all factors must be considered in accounting for the growth of the marsh plants.

An interesting feature of Plot 4, South Glencaple, is the abundance of *Plantago*, while on the surrounding Plot 3, which is somewhat similar in appearance, it is very scarce. This seems to be worth further investigation.

5. *Salicornia*. At none of the four traverses does *Salicornia* appear first on the bare mud, and only at South Glencaple does it grow alongside *Glyceria* as a partner pioneer, if such a term may be used, in the colonisation of the mud flats. It grows further inland, at South Glencaple, along with *Suaeda* and thinly scattered *Glyceria*, with a fair percentage of salt in lower lying plots². A hollow in Plot 4—salt 0.33—grows fine specimens with roots 6 in. long. It is not happy in water-logged places with a high salt content—for instance, plants growing in the wet clayey soil of Plot 4, Kirkconnell, are poor specimens with roots of the average depth of 2 in.

6. *Suaeda*. Remarks about *Salicornia* apply generally to this plant. It is not found as a pioneer plant at any of the four traverses, but usually along with *Salicornia* in lower lying places further inland³.

Fine specimens grow side by side with *Salicornia* in the hollow in Plot 4, South Glencaple.

¹ Marsh (7), p. 81.

² Kearney, etc. (6), pp. 411, 417.

³ Collins (2), p. 383. Oliver (8), p. 13.

7. *Cochlearia*. This grows well with a fairly high percentage of salt, but the salt is not the governing factor. Plant-pot cultivations died early with 2·3 per cent. of salt in the soil. The plants prefer the deep soft mud of the sides of the creeks, especially steep or overhanging sides where the plants get more or less shade. (Roots 7 in. in the creek at Crooks Pow—salt percentage 0·11.) They seem to shun the more open parts of the creeks nearer the river channel. Good specimens are to be found in the shade of *Juncus maritimus* on Plot 6, South Glencaple, but do not occur to the extent described by Marsh, at Holme-next-the-Sea¹.

It is not represented in the vegetation of the dense *Leontodon* plots.

Note. It is well known that *Cochlearia officinalis*, *Armeria maritima* and *Plantago maritima* occur on the higher levels of the Scottish hills, preserving to a considerable extent the characters shown in the salt marshes².

Cochlearia officinalis is also noted in Sir Joseph Hooker's list as one of "the most Arctic plants of general distribution that are found far north in all the arctic areas."

8. *Aster*. A good deal of what has been said about *Cochlearia* would apply in the case of *Aster tripolium*³, but judging from the notes in the table for South Glencaple regarding this plant, and also from its rather plentiful appearance in Plot 4, Kirkconnell, it appears to be better adapted than *Cochlearia* for healthy growth in heavy water-logged soils.

9. *Spergularia*. This plant seems almost confined to loose, deep, wet mud, with a fairly high salt percentage. Compare roots of specimens found on Plots 2 and 4 at Kirkconnell, and on the edge of the pool in Plot 4, South Glencaple. *Spergularia* plants in the pot culture were thriving and in bloom when some of the others already noted were dying or dead. With a salt percentage of 4·42 in the soil, *Spergularia* showed no signs of succumbing to its effects.

10. *Triglochin*. *Triglochin* appears to thrive best in heavy water-logged soils, with a high salt percentage. An examination of the tables will show that it is not found in any of the higher, better drained plots.

SUMMARY AND GENERAL CONCLUSIONS.

From the foregoing observations and determinations the process of colonisation of the mudflats until the vegetation is beyond the influence of the salt water might be stated as follows:

(1) Mudflats exposed at low tide are inhabited by cockles and lobworms and Crustacea. The loose mud is partly consolidated by the shells of cockles, the hardened walls of the burrows of lobworms (and possibly those of Crustacea); by the carapaces of crustaceans such as *Cocophium longipes*, shrimps and crabs; by the droppings of sea-birds and by green Algae.

¹ Marsh (7), p. 82.

² Bower (1), p. 47.

³ Tansley (14), p. 333.

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(2) The height of the flat is gradually raised by sedimentation until it is not submerged by neap tides. Sedimentation then becomes less rapid and consequently the growth of green seaweed becomes more evident.

Consolidation is continued as before, up to this point. Cockles will now be starved out and lobworms will be dwarfed. The crustaceans remain active and by consolidating their burrows permit the aeration of the mud, and consequently its consolidation is assisted, for example, by the oxidation of iron salts.

(3) *Salicornia* may now appear and retain a hold where currents are not too strong to wash away the sediment. Their roots and the parts of their stems that have been buried by new mud will persist and help in consolidation. Also when they rot tubes will remain and keep the soil porous. Lobworms and Crustacea continue to burrow, consolidate and aerate.

(4) When submergence is only by intermediate flood tides, *Glyceria* creeps down among the *Salicornia*, chiefly by its stolons. The old stolons become buried in the mud and thus solidification of the soil is reinforced. The old stolons also keep the subsoil porous. At first, while the plants are sparse, the worms and Crustacea continue. Floating material such as pieces of seaweed, decayed leaves and bits of wood are arrested by the growing *Glycerias* and *Salicornias*, and these all assist in the anchoring of the mud.

(5) *Armeria*, *Plantago*, *Cochlearia*, *Aster*, etc., get a footing when the mud has been sufficiently fixed as indicated above. The vegetation is now becoming "closed." Worms and Crustacea cease to burrow except in the bare or partly clothed hollows. The old roots of *Armeria* and *Plantago* and the old stolons of *Glyceria* keep the soil porous and the burrows of the worms and Crustacea remain as pipes after the creatures cease to inhabit them. When the tidal water sinks air is sucked into the pores. When the tide rises, the used-up air bubbles up. The sea water also has oxygen in solution which is sucked in.

All this time the soil remains slightly alkaline.

(6) The plants of the *Armeria* society continue their upward growth, keeping pace with sedimentation. The merse is now above ordinary neap tides. Vegetation is denser and where it is cropped close by cattle and sheep and geese becomes finer in its growth and presents the lawn-like appearance so noticeable at Kirkconnell.

The nature of the soil is now considerably changed. The droppings of the enormous numbers of curlews, lapwings, sheldrake, geese, gulls, etc., must be very efficient in bringing this about especially as some of these species eat the fish and Crustacea and smaller Mollusca complete with bones, carapaces and shells and thus add lime to the soil.

(7) At this stage inhibition of growth of certain species due to various causes is noticeable. *Salicornia*, *Suaeda* and *Spergularia* are practically choked out by the dense sward. *Glaux* plants tend to become small and short rooted, due to the same cause. Irregularities of the surface, low-lying patches,

portions of the merse in the proximity of creeks resulting in a variation in the amount of salinity, wetness and texture of the soil control the growth of plants, e.g. *Glyceria* seems to grow best with a moderate amount of salt, where the soil is well aerated and the acidity about neutral. It thrives badly in low, water-logged places with a high salinity. The conditions under which various species grow have already been treated fully.

(8) When the sedimentation has raised the level above that of all but storm spring tides, the clay loses its flocculation and porosity, and owing to the consequent want of oxygenation the soil is apt to become "sour." This will happen earlier in the upper reaches of the estuary where the overflowing water at spring tides is likely to be fresh. Occasional submergence by salt water prevents the ground being colonised by earthworms. In absence of artificial drainage, the ground is likely to become a swamp but will support a vigorous growth of vegetation, particularly grass. If the climatic conditions are favourable the swamp will become a peat moss. Where, however, an area of this description is much "poached" by cattle, the effect is a foul, black mud which will not support salt-marsh plants except perhaps *Triglochin* and *Plantago*.

I take this opportunity to express my sincere thanks to the following gentlemen for advice, loan of books and general assistance: Prof. Weiss, Dr Semple, Mr Tansley, Mr G. F. Scott Elliot and Mr R. Leys.

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THE HEATH ASSOCIATION ON HINDHEAD COMMON, 1910-1926¹

By F. E. FRITSCH.

(With seven Figures in the Text.)

THE purpose of the present communication is to summarise the observations that have been made on the heath association on Hindhead Common, S.W. Surrey, to show how far they have helped to explain the diverse character of the vegetation on this comparatively small piece of ground, and to indicate some of the problems that are still outstanding. Two communications dealing with this relatively dry heathland were published in 1913 and 1915 respectively (1, 2); Miss Skipper (3) in 1922 gave an account of the ecology of the gorse, while a valuable study of the soil features by Dr Haines (4) has appeared quite recently. Other special papers are in preparation.

During the period of the war the work was practically suspended, although occasional visits were paid by one or other member of this department. In 1921, however, the investigations were again taken up and pursued vigorously during four consecutive seasons; in spite of the long interval that had elapsed and of the occurrence of a number of fires in the interim, a large proportion of the old stations were located, so that new observations could be definitely related to those previously made in the vast majority of cases. In 1922 Mr H. Glanville of the Engineering Department of East London College prepared a map of the common showing the present position of the footpaths, and a copy of this map accompanies the present communication. While quite especially indebted to Mr Glanville for the labour which he voluntarily undertook, it is a pleasure also to acknowledge the help of my colleagues on the staff of the Botanical Department of the East London College and of the many advanced students who have participated in the work.

1. THE PRESENT CONDITION AND PAST HISTORY OF THE HEATH.

Hindhead Common², and especially the parts lying between points Q and 31 on our base line (see Fig. 1), has now been under more or less continuous observation since 1910. During this period, and more particularly since the war, the frequency of heath fires has increased. There have been some very extensive fires, with the result that practically nothing of the vegetation covering, as we originally knew it, now remains. Considerable areas have been

¹ From the Botanical Department, East London College, University of London.

² The common lies to the south of the main road from London to Portsmouth.

burnt over two or three times during the fifteen years, and data have accumulated to show not only the effects of frequent fires at relatively short intervals, but also the influence of burning of heath of different ages on the subsequent process of regeneration. There can now be no doubt that the patchwork aspect of the vegetation of such heaths as a whole, with its often sharply defined boundaries conditioned by height or nature of vegetation, is largely due to the occurrence of frequent fires of more or less limited range (cf. 1, p. 153). Also that the varied character of the heath vegetation is in great part due to the varying lengths of time that have elapsed since fires occurred on different parts of the ground. It has become apparent that by degrees the sharp boundary line between two fire zones may become blurred and more or less obliterated, probably as a result of the shelter afforded by the taller vegetation and of the consequent more rapid growth of the adjacent members of the lower vegetation (cf. p. 367). Such boundaries tend to become sooner obscured in the sheltered valleys than on the more exposed tops.

It will be useful at the outset to give an account of the history of the central ridge (cf. Fig. 1, and 1, p. 149) to which a large proportion of the subsequent observations relate. When first studied in 1910 (1, p. 152), the top and the whole of the upper slopes were occupied by the C U facies (the approximate lower boundary of which is indicated by the heavy line in Fig. 1); this consisted of dominant tall *Calluna* and innumerable plants of *Ulex nanus*¹ hidden amidst this tall growth. This facies continued right up to the path at the northern end of the ridge, and here and there extended a long way down to, or even actually reached the paths in valleys *A* and *B*. Most of the lower slopes of the ridge were, however, occupied by much shorter growth, representing a region recovered from a former fire about four years back (F 07, cf. p. 347); here *Calluna*, *Ulex nanus*, and *Erica cinerea* were codominant (C U E facies). The exact distribution of these two facies is shown in the map published in 1913 (1, p. 150²). In August of 1911 an extensive tract at the northern end, covering both the C U and C U E facies, was completely burnt (F 11, cf. p. 347), although the fire was stopped at a clearing, at that time running lengthwise along the top of the central ridge; this fire, whose area is indicated by dotting in Fig. 1, also extended a little way on to the opposite slope of valley *A*. The main part of this 1911 fire zone was not burnt again till 1923 (F 23), although the small area on the western slopes of valley *A* was burnt in 1920 (F 20). During the war one or more fires occurred in the adjacent north-easterly part of the central ridge about which no exact data are available.

A further fire (F 16, indicated by dotting in Fig. 1), involving the greater part of the *Erica* slope at the southern end of the central ridge (1, p. 154), occurred probably in 1916 (or early in 1917). This burnt the whole of the

¹ The abundance of *Ulex nanus* on most parts of the ground is a characteristic feature of this and certain other adjacent heaths.

² Cf. also this JOURNAL, 1, p. 216, 1913.

C U E (with dominant *Erica*) in this region and trespassed a little way, but not far, on to the C U facies above; it appears to have been arrested at the steep path leading up to the clearing on the central ridge from valley *A*. The fires of 1911 and 1916 took place on parts of the ground that had already been carefully mapped by the method of square surveys and both regions have since been resurveyed (cf. below).

After the 1916 fire there still remained an extensive tract of the old C U facies extending for some 900 ft. along the top of the ridge, but this was finally swept away in 1924 (F 24) by a fire¹ traversing practically the whole of the central ridge except for the northern portion which had already been burnt in 1923 (F 23). The map published in 1913 is thus purely of historical interest and, except at a very few points, no longer indicates the distribution or condition of the vegetation.

Similar radical changes have, however, occurred over most of the common. Except for the wooded region at the southern end adjacent to the Farnham Lane (2, p. 137) there can only be small areas that have not been affected by fires since the vegetation of the common has been studied. Thus, nearly the whole of the slope facing the *Erica* slope and forming the southern boundary of valley *B* was burnt, probably at the same time as the *Erica* slope in 1916 (F 16a). There have also been repeated fires on the eastern slopes of valley *B*, one rather considerable one taking place in 1922 (F 22) and another farther down the valley in 1926 (F 26). The western slopes of valley *A* were burnt in 1920 (F 20), this fire extending over part of the 1911 fire zone and also including an area burnt in 1909. The old F 2 in valley *C* (2, p. 117; F 12 on the present map) was unaffected by fires for a long period and has afforded some interesting data, but was completely eliminated in 1924. The burnt area in valley *D* (1, p. 117) still persists and in 1924 had advanced to the stage of a typical C U E facies, but the upper part was invaded by a fire from the adjacent ridge in 1918.

In the appended summary of the different burnt areas, to which reference has been made and which will be frequently mentioned in the following, the method of designation adopted in the 1915 paper (2, p. 117) has been abandoned. Each area is indicated by F followed by a number denoting the year (as nearly as it can be ascertained) in which burning occurred. Thus, F 18 represents an area burnt about 1918. The areas in question are as follows:

- F 07. The old C U E facies on the slopes of the central ridge (more or less extensively reburnt in 1911, 1916, 1923, and 1924). (F 7 of the 1915 paper.)
- F 09. The F 5 of the 1915 paper and probably all included in F 20 (see below).
- F 11. The F 3 of the 1915 paper, reburnt in 1923 (F 23).
- F 12^a. The F 2 of the 1915 paper, reburnt in 1924.

¹ This fire was intentional on the part of the authorities entrusted with the care of the Common. It also attacked the vegetation on the more or less bare gravel areas on the eastern slopes of the central ridge, but here much was left unburnt.

² In the map published by Haines (4, p. 35) this area was shown in the wrong position.

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- F 13. The F 1 of the 1915 paper, upper part burnt again in 1918 (F 18); in 1924 F 13 bore a typical C U E facies (F 13 lies just beyond the extreme right of the map, Fig. 1).
- F 16. The area on the *Erica* slope, at the south end of the central ridge, burnt approximately in 1916 and reburnt in 1924 (F 24).
- F 16a. The area on the slope opposite the *Erica* slope and probably burnt at the same time (in 1916, but not in 1924).
- F 18. An area near the top of F 13 in valley *D* (outside the map).
- F 20. An area on the W. slope of valley *A*, probably including F 09; aspect E.S.E.
- F 22. An area on the E. slope of valley *B*, aspect W.N.W.
- F 23. An area at the north end of the central ridge, burnt early in 1923, extending over and beyond F 11 in an easterly direction.
- F 24. The area burnt in 1924 and extending over practically the whole of the central ridge (except part covered by F 23), including F 16.
- F 26. An area on the E. slope of valley *B*, adjacent to F 22.

The location of the different burnt areas is shown in the accompanying map (Fig. 1). It will be noticed that there are some parts of the common in which burnt areas are not indicated. This must not be taken to imply that they have not been burnt during the period of observation, but lack of time precluded a keeping of records for the whole common from this point of view.

Before proceeding to detailed considerations it may be well to recall that the vegetation of Hindhead Common is exceedingly poor in species, except along the pathways. Over great areas of the common one finds only *Calluna*, *Erica cinerea*, *E. tetralix*, *Ulex nanus*, *Vaccinium Myrtillus*, and *Pteridium*; the only common grasses are *Molinia coerulea* and *Aira flexuosa*. Of the many species met with along the paths (2, p. 133) few are ever found more than a few feet away from them, except on newly burnt areas.

2. THE RETURN OF BURNT AREAS TO A RELATIVELY STABLE CONDITION.

Since the vegetation of a considerable part of the common had been carefully mapped prior to 1914, the condition of various burnt areas before the occurrence of the fires was accurately known. When work was taken up again after the war, a new survey of a number of such regions, in which many years had elapsed since the last fire and in which the vegetation had practically closed up and was rapidly reaching the condition of the mature heath, was undertaken. Two of these regions are selected for a comparison of the condition of the heath before and after burning, viz.:

(a) An area 400 × 100 ft. (about 122 × 30.5 m.) on the western slopes of the central ridge¹, with a W.N.W. aspect, burnt in August 1911 (F 11) and resurveyed in July 1921, having been kept under observation in the interim (Figs. 2 and 3).

(b) An area, roughly 400 ft. (122 m.) square, situated on the S. slopes of the central ridge (*Erica* slope)², burnt in 1916 (F 16) and resurveyed in July 1922 (Figs. 4 and 5).

Two general facts emerge from a comparison of the different charts, viz. the stationary character of the bulk of the vegetation and the spreading of

¹ Between points 4 and 7 on the base line and extending 100 ft. from it up the slope.

² Roughly between points 17 and 21 on the base line (see Fig. 4).

certain constituents. Taking first the area (a) above specified (cf. Figs. 2 and 3), it is to be noticed that the fire (the lower limit of which is marked by the heavy line in Fig. 3) swept across the old boundary of the C U and C U E facies (itself a fire boundary, cf. Fig. 2). Part of the old C U E facies was however left untouched, but by 1921 (Fig. 3) this had progressed to the C U stage, the

FIG. 2. 1911

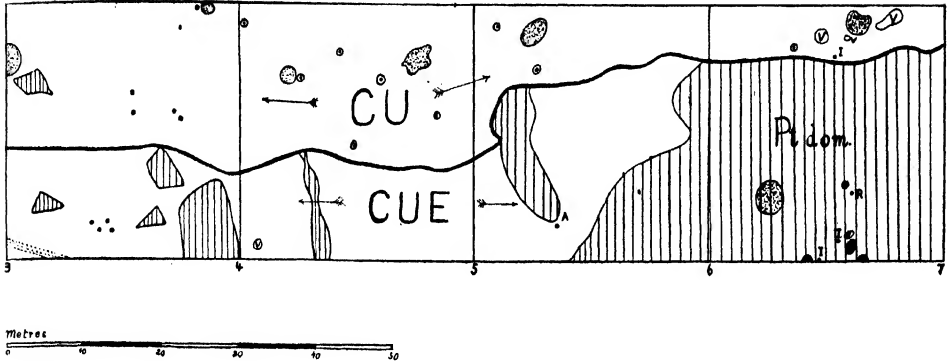
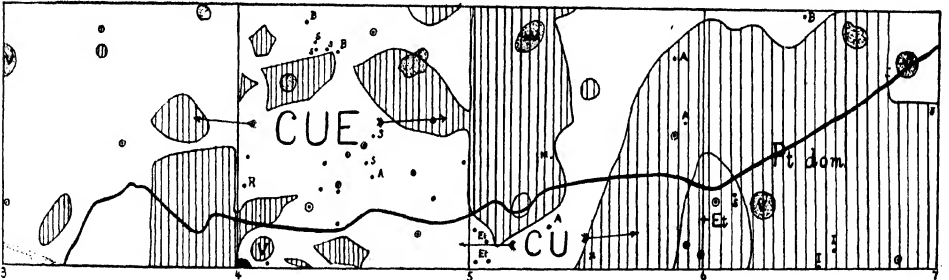


FIG. 3. 1921



FIGS. 2 and 3. Charts showing the distribution of vegetation in four consecutive 100 ft. (30.5 m.) squares on the same area of ground on the western slopes of the central ridge, along the base line (consecutive points of which are indicated by the numerals), in 1911 and 1921 respectively; a great part of the area shown in the upper chart (Fig. 2) was burnt, after mapping, in August 1911, the lower boundary of the fire being shown by the heavy line in Fig. 3. The heavy line in Fig. 2 represents the boundary between the C U and C U E facies, as it existed prior to the fire. Areas with abundant bracken are indicated by shading, hollows by dotting, unnamed dots indicate isolated small *Pteridium* patches, ringed dots young plants of *Pinus*. A = *Pyrus aucuparia*; B = *Betula pubescens*; Et = *Erica tetralix*; I = *Ilex aquifolium*; R = *Rhamnus frangula*; S = *Pyrus aria*; V = *Vaccinium Myrtillus*.

Erica cinerea plants having become relatively scanty and inconspicuous. On the other hand the region formerly occupied by the C U facies (Fig. 2) was now replaced by a C U E facies, with *Erica cinerea* playing a conspicuous part. In other words, a complete inversion of the relative positions occupied by the two facies had taken place, and this furnishes direct evidence, if indeed any is still required, that the two facies are not due to habitat- or soil-conditions, but

merely represent successive phases in the maturation of the heath after a fire (1, p. 160).

The relations of the bracken (whose distribution is shown by shading in Figs. 2 and 3) to the two phases is also of interest. There is undoubtedly an increase in the total area occupied by the fern, but this is in the main within the burnt region. Bracken does not seem to be able to make much headway in the older heath below the fire boundary (Fig. 3), and the way in which even extensive areas (cf. Fig. 2) were held in absolute check at the C U boundary in 1911, but have spread considerably after this barrier was removed by the fire, is very striking. A great factor in the spread of bracken, at least on this common, are the occasional hollows (shown dotted in the two charts) that are to be encountered. These owe their origin generally to the removal of burnt trees, which are taken out with their roots, and probably as a result of their greater moisture content and shelter are very frequently colonised by bracken. A number of the new *Pteridium* patches in the 1921 chart (Fig. 3) have obviously originated amid such hollows. Their frequent colonisation by bracken after fires has been noted also on other burnt areas on the common. *Vaccinium Myrtillus* likewise commonly settles in such hollows and one may find a plentiful crop of whortleberry plants there, when there are practically none round about.

Turning now to the other pair of charts (Figs. 4 and 5), representing the area (b) mentioned above, that made prior to 1914 (Fig. 4) again includes the boundary between the old C U and E U C facies (with *Erica cinerea* dominant). The fire however (cf. Fig 5) swept right across this boundary and seems to have extended down to the path in the valley. It was stopped at the ruts, marking a rough pathway in the upper left-hand corner of the chart (Fig. 5, the heavy line marks the fire boundary). Attention may first be drawn to the fact that outside the limit of the fire (left-hand top part of Fig. 5) the *Calluna* has become dominant; also there is a marked increase in the size of the *Pteridium* (shaded) and *Molinia* (dotted) patches, but no increase in their number. Neither probably settle down easily in a more or less closed community. In the region of the fire, however, marked changes have occurred. The main gorse and bracken areas adjacent to the path are recognisable in both charts and no obvious increase of *Ulex europaeus* has taken place. Both *Pteridium* and *Molinia* have however appreciably extended their domain. The irregular dotted line in both charts marks an upper zone above which bracken fronds were not frequently encountered, although two extensive patches of bracken situated above this boundary are indicated in Fig. 4. It is very noticeable that the upper boundary of scattered *Pteridium* in 1922 (Fig. 5) roughly corresponds to the line marking the lower limit of the C U facies in 1914 (Fig. 4). It was here that the spread of bracken was held up prior to 1914 (cf. above), and it has apparently been unable to appropriate this ground even after the fire, since a large part of the *Erica* slope above this

point bore in 1922 only very occasional *Pteridium* patches (Fig. 5). On the other hand, below this line it has now spread, though rather thinly, over most

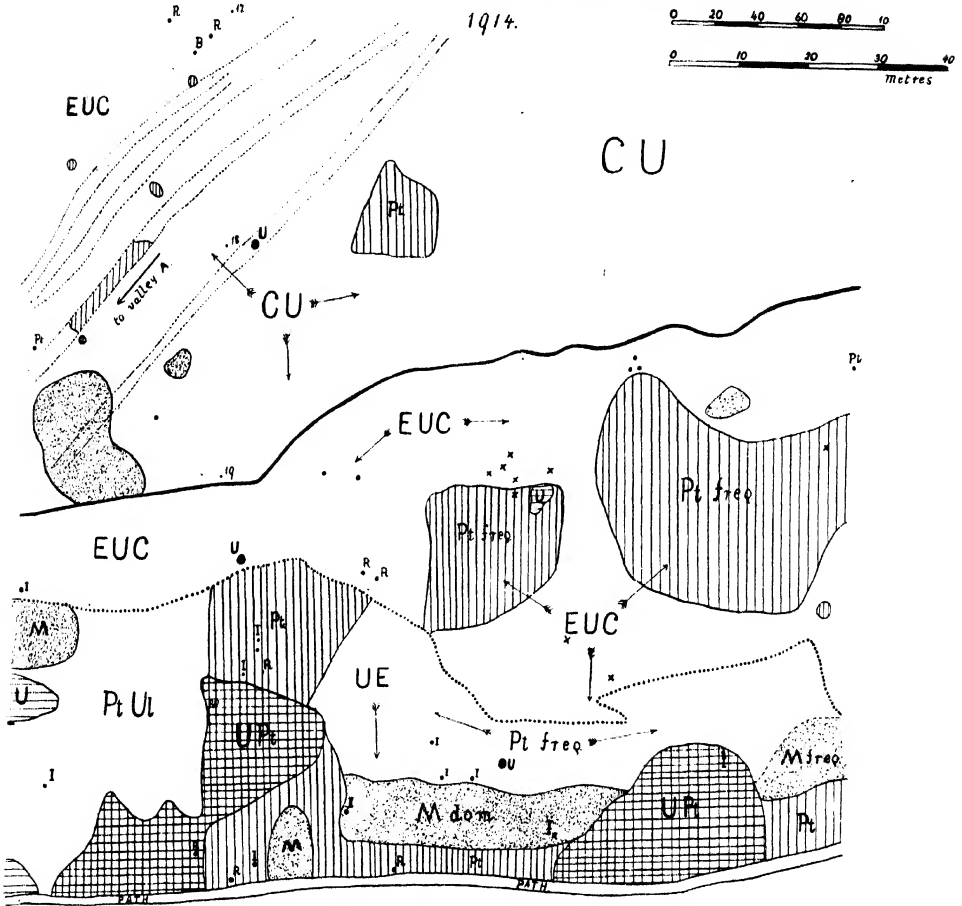


FIG 4. Chart showing the distribution of the vegetation on part of the lower portion of the *Erica* slope in 1914. The numbers 17, 18, 19, 20 indicate successive points on the base line. The finely dotted lines in the upper left-hand part of the chart show the positions of a number of ruts marking a rough pathway leading up to the top of the central ridge from valley A. The heavy line shows the boundary between the C U and E U C facies, the coarsely dotted line shows the upper limit of frequent bracken. Bracken is indicated by vertical, gorse by horizontal shading, *Molinia* patches by dotting; crosses mark the positions of isolated *Ulex europaeus* plants, unnamed dots indicate isolated *Molinia* plants. B = *Betula pubescens*; I = *Ilex aquifolium*; M = *Molinia caerulea*; Pt = *Pteridium*; R = *Rhamnus frangula*; U = *Ulex europaeus*; Ul = *Ulex nanus*.

of the ground and further fires will probably lead to its becoming quite a dominant feature in this region.

The results as regards the bracken, both in this area and the one above considered, show that within the closed heath association extension of area

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occupied by existing *Pteridium* patches may take place, but that new patches do not readily establish themselves. But on burnt areas a certain number of new plants may arise, especially where hollows in the ground, such as are left by the removal of trees, facilitate their development, and these may then serve

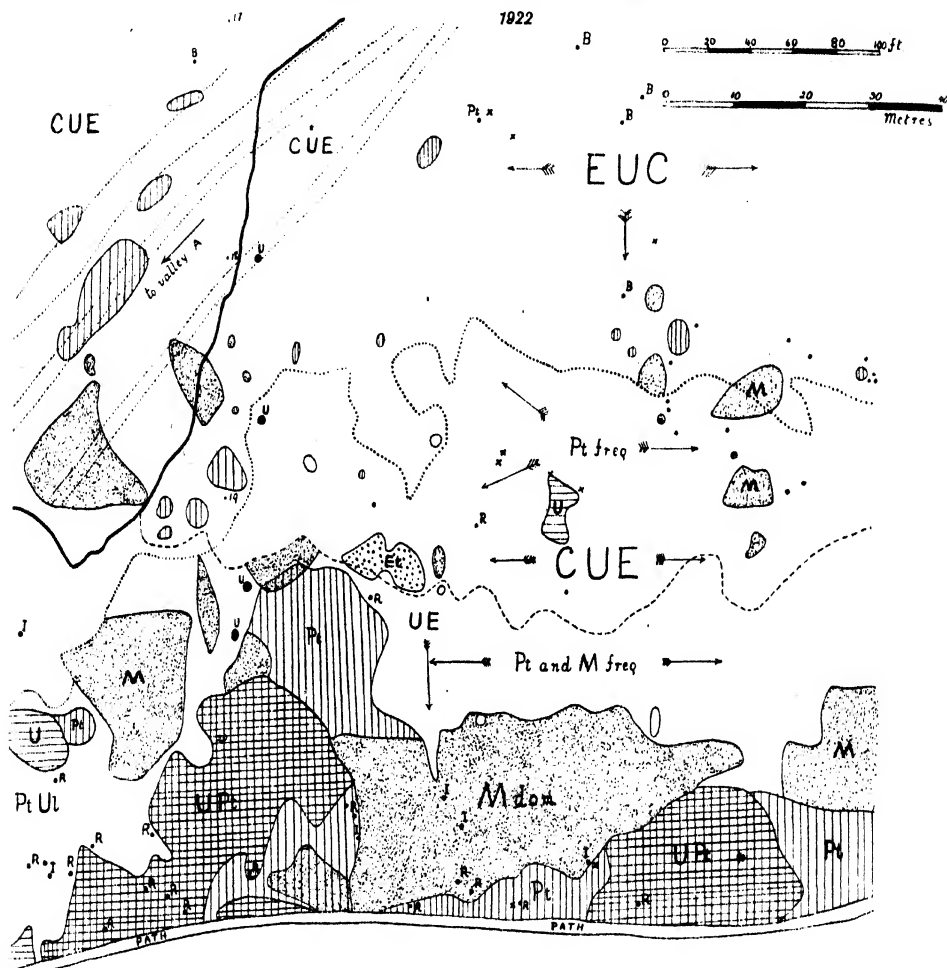


FIG. 5. Chart showing the distribution of vegetation on the same area as in Fig. 4 in 1922 (the area in question having been burnt in 1916). The heavy line shows the boundary of F 16. The interrupted line in the lower part of the chart marks the upper limit of abundant *Molinia*. Method of representation and symbols the same as in Fig. 4.

as centres from which the surrounding heath is slowly invaded. This invasion is however at most points but a slow process and the actual change in the distribution of bracken, in the two zones considered, over a period of ten years relatively small. That the change is slight is also shown by studying the distribution of the individual bracken fronds over small pieces of ground in

successive years (cf. p. 354). There are indications that at times an opposite tendency may prevail, as for instance is shown by the occasional decrease in size or disappearance of *Pteridium* patches, as on the left-hand side of Fig. 3 and the upper part of Fig. 5.

On the second area a very obvious spread of *Molinia coerulea* has also occurred. In 1914 (Fig. 4) this grass was very largely confined to the neighbourhood of the path, being more or less dominant at some points and at others (not specially indicated in the chart) in competition with gorse and bracken. About 50 ft. above the path, however, it was but rarely to be met with and the majority of the tussocks were of small dimensions with only four or five inflorescences. Here and there a larger one was to be found (shown by unnamed dots in Fig. 4), and near the C U facies on the right there was one quite extensive patch¹. After the fire the *Molinia* spread apace, greatly enlarging its area of dominance adjacent to the path (cf. Fig. 5) and extending for a considerable distance up the slope; the interrupted line in Fig. 5 provides a boundary below which *Molinia* plants are too frequently present to be marked individually, as has been done above that boundary. It is to be noted that not only have the *Molinia* patches already present before the fire undergone great enlargement in most cases, but there are plentiful new patches and isolated tussocks above the boundary of frequent *Molinia* that promise a further spread after the next fire. It does not seem that, after a certain stage, new *Molinia* plants easily establish themselves on the closing heath in competition with the ericaceous forms and *Ulex nanus*, but once they have got a hold on the ground they are probably able to maintain themselves by virtue of the dense growth of their tussocks and the shade they cast over their lower-growing neighbours. It would seem that, when the ground is suitable in other respects, *Molinia* will spread more quickly after a fire than the bracken (cf. also p. 356).

Although the two pairs of charts thus show certain changes, they are perhaps more striking because of the little alteration they exhibit. *Pteridium* and *Molinia* patches occur where they occurred before the fire, the *Ulex europaeus* stretches adjacent to the paths persist, the ericaceous forms appear in the same groupings as before the fire, many of the isolated gorse, holly, etc., bushes survive² to grow up in the same spots. The relative stability here recognisable would however be *much more* pronounced on other parts of the common, where there are no large masses of adjacent bracken to extend over the burnt zone (as in the case of the area (a) above) or which are not located near the valleys, from which *Molinia* can spread. The areas depicted in Figs. 2-5 have been selected because they indicate change and it has not been deemed necessary to reproduce charts in which no appreciable difference in the vegetation before and some years after a fire is apparent.

¹ To the right of the area represented in Fig. 4, *Molinia* was already rather abundant prior to F 16.

² The absence of some is doubtless due to removal.

3. FURTHER OBSERVATIONS ON THE SPREAD OF *PTERIDIUM*, *MOLINIA*, AND OTHER FORMS.

The behaviour of bracken and *Molinia* has also been studied by mapping, in successive years, the distribution of individual plants on small areas of the ground. Fig. 6 shows the distribution of the individual bracken fronds on an area approximately 12 ft. (366 cm.) square near the top of square 3 A in valley A in 1922, 1923, and 1924 respectively; the irregular line circumscribes one of the larger hollows above referred to. The three charts show four features, viz. (1) that such hollows constitute centres from which the surrounding heath is invaded, (2) that the direction of growth of the bracken on such a small area is uniform and in this case always down the slope (indicated by the arrow), (3) that there is no appreciable increase in the number of fronds in 1923 as compared with 1922, and (4) that there is a very great increase in 1924, after the fire of 1923.

It has been impossible to find, except in very few cases, evidences of the origin of new bracken plants from prothallia and such were nearly always observed in damp hollows¹ like those here referred to (cf. 5, p. 224; 6, p. 135). It is not denied that such spore development may occasionally take place also on the flat surface of the heath, but it is certainly uncommon and new areas of bracken are probably essentially due to spore germination within the shelter of hollows and other depressions of the ground. On young heath one may occasionally observe an isolated bracken frond emerging from the midst of a dense cushion of *Ulex nanus*; such fronds are often many feet away from any others and their small size suggests that they belong to young plants. If spores of the fern are blown into such cushions they may, within the shelter of the dense tangle of branches, find the necessary amount of moisture for the production of a prothallus and an embryo (cf. 6, p. 136).

On young heath, before there is a dense matting of the roots, etc., of the ericaceous forms, growth of the rhizomes would appear to be fairly rapid, new fronds appearing often 2-3 ft. in advance of the old ones of the previous season, but as the heath closes this rate of progression greatly diminishes. Moreover, it is only in the very first years after a fire that abundant branching of the rhizomes appears to take place, with resulting vegetative propagation and increased production of fronds. In later stages one may often find corresponding to almost every living frond a dead one of the last season, and the new one often comes up at practically the same place as the old one. On the maturer parts of the heath it has not uncommonly been noted that bracken fronds fail to appear in the following year over small stretches of the ground, so that there

¹ Also in ruts along the pathways in the valleys where bracken is always to be found in abundance and which no doubt constitute the main areas from which invasion has taken place. In this connection it is significant that the only extensive regions over which bracken is completely lacking are on the flat summit of the central ridge which is most remote from the pathways.

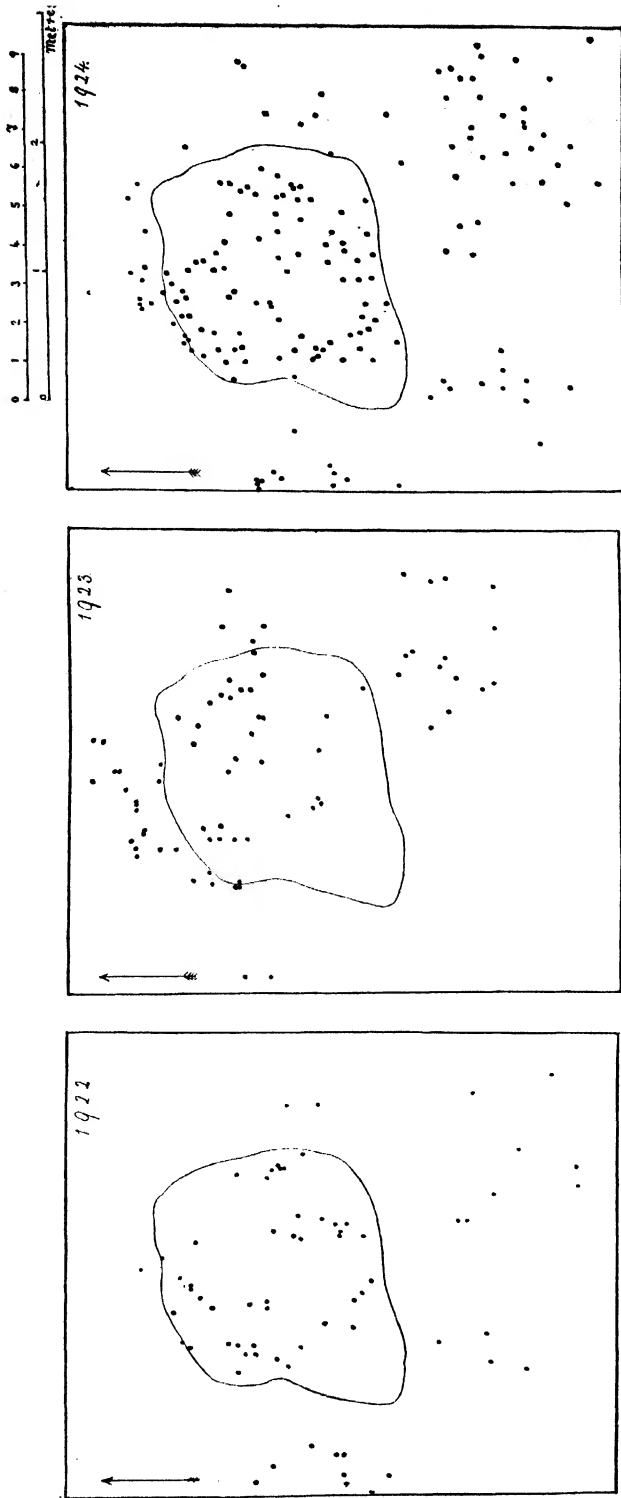


FIG. 6. Charts showing the distribution of the individual bracken fronds on a small area of the heath in three successive years; the charts which are portions of larger ones were prepared in the month of July in each year. The area in question was burnt early in 1923 (F 23). The irregular line indicates a large hollow in the ground, the arrows point down the slope.

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may be an actual retrogression (cf. also Table I), although the exact cause is not at present apparent.

Table I. *Numbers of bracken fronds on different 25 ft. (7.6 m.) squares in successive years.*

Position of square	1922	1923	1924
1. W. slope of central ridge (valley A), burnt early in 1923	85	107	200
2. A similar area, close at hand, burnt at the same time	95	112	211
3. Upper part of <i>Erica</i> slope, burnt in 1924	127	91	89
4. A similar area close at hand	353	288	—

Such retrogression has only been observed in regions in which *Pteridium* is sparse and there is no evidence that it obtains where the fern is a dominant. On any small area of ground that may be examined, however, there is always an increase in the number of *Pteridium* fronds in the year succeeding a fire (cf. Fig. 6 and Table I), although owing to the rapid slowing down in the rate of growth in the subsequent years, much actual spread is not effected except where there are already present extensive masses of the fern. The tendency for the growth of all the plants over a small circumscribed region to take place in one direction (often down, but sometimes up slopes or occasionally along them) is a feature frequently noted on the common, but for which there is at present no explanation.

The grass *Molinia coerulea* is essentially confined to the bottoms of the valleys from which it is invading the slopes at many points. It does not appear however that such invasion can occur to a serious extent except in the first years after a fire; moreover, whereas all parts of the heath are probably favourable for the growth of *Pteridium*, *Molinia* can only settle where the soil conditions are suitable. Thus, whilst a steady invasion of the *Erica* slope by *Molinia* is taking place from below (cf. p. 353 and Figs. 4 and 5), and this grass is spreading extensively on the gravel areas on the E. slopes of the central ridge, it is by no means spreading at all points where it occurs on the common. At the northern end of the central ridge round about the point 0 on the base line, where a slight depression of considerable extent occurs, a quantity of *Molinia* has been a striking feature during the whole period of our observations, but although the adjacent terrain has been burnt repeatedly there has been no marked extension of the area of the grass. Both Jeffreys (6, p. 137) and Haines (4, p. 65) emphasise the occurrence of this grass in regions rich in humus and characterised by a high acidity and such soil factors may well be mainly operative in limiting its spread.

Where the ground is suitable, small plants of *Molinia* are to be found among the members of the mature heath well in advance of the main zone of occurrence. It does not seem, however, that such plants are able to establish them-

selves as vigorous tussocks against the competition of *Calluna*, *Erica*, etc., and they remain small with only a few inflorescences. Such was the condition of the plants, for instance, in the small area near the base of the *Erica* slope depicted in the left-hand chart of Fig. 7; above the region shown even such plants became fewer and fewer till they disappeared altogether. A slight increase in the number of plants and in the size of some of them was recorded in 1923, but in 1924 (see the right-hand chart in Fig. 7), after the ground had

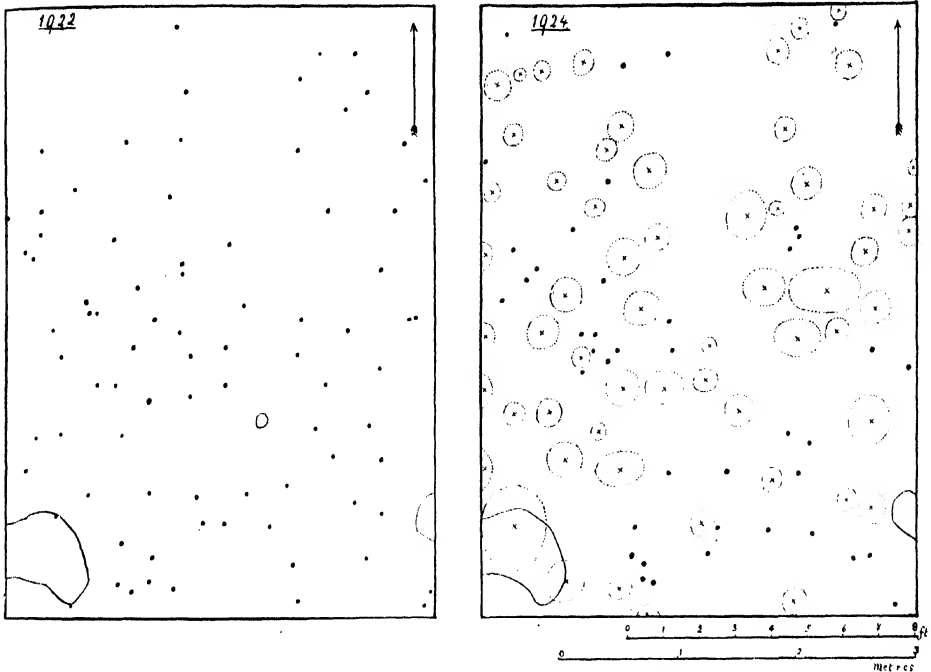


FIG. 7. *Molinia coerulea*. Charts showing the distribution of individual plants (indicated by dots) and larger tussocks (indicated by a cross surrounded by a dotted line—some of these possibly comprising two or more plants) on a small area near the base of the *Erica* slope in 1922 and 1924; both charts are portions of larger ones and both were made in the month of July. The area in question was burnt early in 1924. The arrows point up the slope. The undotted lines mark the boundaries of hollows in the ground.

been burnt, these tussocks exhibited a very great enlargement and by spreading out over the soil rendered colonisation by ericaceous forms impossible in their immediate vicinity. It may be noted that *Molinia* exhibits considerable spread in the year of the fire (if the latter occur early), whilst bracken always only spreads in the year succeeding a fire.

The only other grass that occurs at all frequently in the closed heath is *Aira flexuosa* (1, p. 154). It is found most abundantly along the pathways, not only those in the valleys but also those on the ridges. On the whole it and the *Molinia* are to a considerable degree mutually exclusive; even in the valleys

this is true to some extent, for the *Aira* occurs along the edges of the paths, while the *Molinia* occurs beyond them at the bases of the slopes. The feature in question is very patent on the gravel areas on the E. slopes of the central ridge, where these two grasses are very abundant, but where the one is frequent the other is scarce and *vice versa*. There are some extensive areas of *Aira* on the top of the central ridge and on the upper part of the slopes opposite the *Erica* slope (F 16a in Fig. 1); in both situations the other grass is wanting, while *Aira* is absent from the special *Molinia* zone round point 0 (cf. above). It is probable that conditions are suitable for the growth of *Aira* over large parts of the heath¹ and isolated specimens are indeed to be found at most points, but except where they occupy small gaps in the vegetation covering (bare areas?, cf. below) they do not seem to survive competition with the other plants. *Aira* is of course not nearly as aggressive as *Molinia*; it does not develop dense tussocks and is less robust in habit. This explanation of its relative scarcity in the mature heath probably also applies to *Agrostis vulgaris*, which is often found together with *Aira* along the paths and sometimes on recently burnt areas (cf. 2, p. 133).

Another plant that evidently effects little spread is the Dodder (*Cuscuta epithymum*)². There is usually a very extensive growth of this (comprising several square yards of densely infected plants of various kinds) round about point 0 on the base line. Similarly, there is generally a good deal of this parasite near the path at the base of the *Erica* slope, but from neither region does there seem to be much spread except when the adjacent ground is newly burnt. This may in part be due to the inability of the seedlings to attack other than young growth, but would not explain the absence of the parasite on areas with rich bracken, whose fronds are especially liable to attack on freshly burnt ground. New burnt areas sometimes look deep rust red from afar owing to the abundance of Dodder plants that are present.

Two other plants, belonging to the heath flora, viz. *Vaccinium Myrtillus* and *Erica tetralix*, do not appear to have appreciably altered their area of distribution during the period of observation. Both are met with especially near the bases of the slopes and are wanting over considerable areas of the tops, but there are marked anomalies in their distribution which have been dealt with by Haines (4, pp. 64, 66) though not fully explained. The big areas of *Vaccinium* on the southern part of the top of the central ridge are possibly in part due to the rapid regeneration of this plant after fires (6, p. 141).

¹ The soils from the special *Aira* zones do not differ fundamentally from those found over most of the tops (4, p. 66).

² Attention has already been called to the fact that this parasite attacks practically all the members of the heath flora (2, p. 132). On a small stretch of burnt ground in valley B it was in 1926 found attacking a specimen of *Orchis maculata* that had settled there.

4. FURTHER OBSERVATIONS ON THE RECOLONISATION OF BURNT AREAS.

Observations made on the central ridge in July, 1924, after the extensive fire (F 24) early in the year, have led to some modifications in the views formerly expressed as to the mode of recolonisation of burnt ground on Hind-head Common. At the date named, proceeding from the path at the base of the *Erica* slope upwards in a northerly direction over the top of the ridge until one reached its northern extremity, four different types of burnt ground were to be encountered, viz.:

1. The *Erica* slope, whose vegetation at the time of burning (early in 1924) was about 7 years old and still relatively low.

2. The extensive C U facies extending from the top of the *Erica* slope to within about 700 ft. (213 m.) of the northern end of the ridge. The vegetation over the whole of this region had been very tall prior to the fire and had not been burnt for some 25 years.

3. A narrow zone of F 11, occupying a stretch extending approximately between 700 and 550 ft. (213 and 166 m.) from the northern extremity of the ridge. The growth here prior to the fire was about 12 years old, but owing to the greater exposure was not much taller than that on the *Erica* slope.

4. The remaining 550 ft. (166 m.) of F 11, which was burnt in 1923 and not affected by the fire of 1924.

Here therefore it was possible to compare recolonisation on heath of very different ages and with different exposures. The various zones will be taken successively.

(1) In striking contrast with earlier observations (1, p. 158; 2, p. 119) it was found that a very large number of the *Calluna* and *Erica cinerea* plants on the *Erica* slope were sprouting from the old stools. Even quite small plants, that could have reached no great size before the fire, were sprouting and that vigorously; this was particularly true of *Erica cinerea*. The only *Calluna* plants that appeared dead were some of the larger older ones. The latter, however, even when sprouting, only showed a feeble growth of a few shoots, whilst most of the younger plants had already formed dense cushions¹. This would seem to imply that the age of the plant had something to do with its capacity for regeneration, but the effect is probably indirect. Over most of the common where growth of tall *Calluna* occurs, one can find young plants among the older ones and yet, when such a region is burnt, very few *Calluna* plants are subsequently found to be sprouting (cf. 1, p. 158 and zone 2 below). It seems more likely that the observations on the *Erica* slope, just detailed, are to be explained as a result of the amount of heat generated and the duration of heating when a large plant is burnt. Where, as on the *Erica* slope before the fire, only

¹ This finally disposes of the suggestion (1, p. 159) that depth of rooting conditions the selective killing by a fire.

a few of the plants here and there were tall, these will have suffered more than their lower-growing neighbours. Where, however, as in other regions (cf. zone 2 below) the bulk of the growth is tall, the total heat generated is enough to kill off the majority of the *Calluna* and *Erica cinerea* plants, both old and young. As a matter of fact many of the smaller *Calluna* plants on the burnt *Erica* slope under discussion had only been scorched by the fire, as some of the brown scorched shoots were still evident upon them. The rapidity of travel of the fire is also indicated by the fact that several unburnt patches were left near the top of the ridge.

As a result of previous examination of burnt areas it was concluded (2, p. 120) that only those plants survive burning in which either the branching of the crown takes place beneath or in close contact with the surface of the soil (*Ulex nanus*, some *Calluna* and *Erica cinerea*), or those in which, although branching occurs above the surface, it is so profuse as rapidly to accumulate a mound-like protective covering of humus (*Erica tetralix*, *Molinia*, *Carex pilulifera*). A large number of the *Calluna* plants on the *Erica* slope certainly had buried crowns which was perhaps a result of the slope and the consequent tendency for detritus to be washed around the stems. But by no means all the sprouting specimens had buried crowns and this was specially the case with the young *Calluna* and *Erica cinerea* plants which were sprouting most vigorously.

A peculiar feature of the older *Calluna* plants on the *Erica* slope was very obvious after the fire. The lower part of the main stem was usually prostrate, the stems being always directed *up the slope*. Some of the branches formed on the lower side of the prostrate stem thus become buried in débris and it was from these that sprouting was often taking place. The prostrate stems of the *Calluna* were sometimes found to have taken root and it is possible that some of the small plants found growing between the larger ones on old parts of the heath may arise in this way, although many are certainly produced from seedlings.

For the rest the burnt area on the *Erica* slope showed the features customary a few months after a fire. *Ulex nanus* was sprouting from the old stools as usual and all of the few seedlings present belonged to this plant. A very striking feature of this burnt area on the upper part of the *Erica* slope was the practical absence of all casualties (except for one *Potentilla erecta*), a condition very unusual in the first year succeeding a fire; the vegetation consisted almost solely of *Calluna*, *Erica cinerea*, *Ulex nanus*, and occasional *Pteridium*¹. This is probably to be ascribed to the region in question being situated some distance away from the paths, so that the source of infection was remote, but it may also be connected with the direction of the prevailing winds.

(2) On entering the old C U zone on the top of the central ridge, the burnt area presented a very different picture. In this tall growth the fire must have

¹ No *Vaccinium Myrtillus* or *Erica tetralix* occur in the region under discussion.

raged very fiercely and everything was practically completely burnt¹. The state of the vegetation resembled that described in the earlier accounts (1, p. 156; 2, p. 119). *Ulex nanus* and *Vaccinium* were sprouting everywhere, but a large number of the *Calluna* plants gave no indication of life at all; those that were sprouting invariably had buried crowns, but even such plants were often dead. Very little sprouting *Erica cinerea* was to be seen. Taking it as a whole the ground was here not nearly as completely covered with green growth as on the *Erica* slope (cf. (1) above), although both had been burnt *at the same time*. This alone shows the effect of the greater intensity and duration of the heat generated by the burning of the much taller growth.

The big tussocks of moss (*Hypnum cupressiforme* var. *ericetorum*, *Leucobryum glaucum*) that are to be found mainly about the bases of the *Calluna* stems in the older growth such as occurred on this part of the common, persist as large charred masses, but seem always to be completely killed by the fire.

(3) In this third zone the new growth was again much denser and much more like that on the *Erica* slope, the contrast between zones 2 and 3 in this respect being recognisable already from afar. As above mentioned, the vegetation here, although considerably older, was not much taller than that on the *Erica* slope prior to the fire. The heat of the latter will therefore have been of much the same intensity and certainly appreciably less than in zone 2, the more so as there were practically no trees in the region under discussion. The fact that a large number of the *Calluna* and *Erica cinerea* plants were again found to be sprouting is important evidence in favour of the contention above made. That the heat of the fire had been inconsiderable was shown also by the fact that some of the dense *Ulex nanus* cushions were not only sprouting from the buried crowns, but also from the lower parts of some of the upright shoots forming the convex cushion (2, p. 125). It may be that such specimens are the ones subsequently to produce a number of upright shoots (2, p. 126) which during their early growth are protected by the burnt mass of the old cushion.

(4) This zone, being rather more than a year in advance of the others (F 23), was already showing signs of closing up. The growth had however at the time of the fire been of about the same height as on zone 3 and here again large numbers of the *Calluna* and *Erica cinerea* plants were sprouting. An interesting point of contrast between this zone and the others was afforded by the fact that *Erica cinerea* was in full flower here, but not in the other zones; it appears that it does not flower in the first year succeeding a fire and this is probably largely true of many of the other heath constituents.

All the facts point to the necessity of modifying the earlier conclusion with reference to the survival of *Calluna* and *Erica cinerea*. Whether these forms rejuvenate or not depends in the first place on the height of the vegetation

¹ The rather frequent trees found in this region will also have contributed to the intensity of the fire.

burnt and the resulting amount of heat generated. When the heat is intense, only those plants with buried crowns survive and not all of these. It would also seem that *Ulex europaeus*, if the fire has been very fierce, may fail to sprout. On the other hand, the majority of the *Ulex nanus* plants always survive, no matter what the intensity of the fire has been.

The region occupied by F 12 (the F 2 of 2, p. 117), which was reburnt in 1924, was then 12 years old. Occupying a somewhat sheltered slope the vegetation was on the average a good deal taller than that of almost equivalent age (F 11) on the summit of the central ridge (zone 3 above) and the effects of the fire correspondingly greater. In July 1924 *Ulex nanus* was sprouting extensively, also quite a number of the *Calluna* and *Erica cinerea* plants; of the last two however there were not nearly as many as on the *Erica* slope with a similar exposure. Again it was apparently especially the larger plants that had been killed by the fire (cf. above). The *Erica* was not in flower.

The different zones of F 24 (and F 23) were re-examined in June of 1926, two years after the fire. At this time the contrast between zones 1 and 2 was so startling that one would be inclined to believe that the latter had been burnt much more recently than the former (cf. also p. 365). In zone 1 the vegetation had already practically closed up and had reached a height of about a foot, whilst in zone 2 there were large bare areas and the growth was still quite open and low. In this latter zone much of the charred surface of the soil was visible, although the ground between the sprouting *Ulex nanus* plants was often covered with small seedlings of *Calluna* and *Erica cinerea*. The two zones moreover contrasted sharply in the fact that in zone 2 the Dodder was quite abundant and there were a considerable number of casuals (e.g. *Epilobium angustifolium*, *Hypochaeris radicata*), all of which were lacking in the first zone. That the open character of the vegetation in zone 2 was not a result of its location on the top of the ridge and its consequent greater exposure, was shown by the fact that the same type of vegetation could be followed right down to valley A, wherever the old C U facies had extended far down towards the path.

Zone 3 presented much the same appearance as zone 1, although the vegetation was perhaps a trifle more open. Zone 4, although a year older than the others, was scarcely to be distinguished from zone 3. The vegetation was still relatively open and not quite as tall as in zone 1. This is no doubt a result of the greater degree of exposure on the top of the ridge, since in the part of zone 4 that extended down the slope into valley A the growth was much denser and about twice the height of that on the top (cf. p. 367).

The appearance of a burnt area some two years after a fire thus depends (a) on the height of the vegetation that was burnt, and (b) on the degree of exposure of the ground. The burning of tall growth, or alternatively considerable exposure, lead to the prolonged persistence of an open type of vegetation in which colonisation by casuals is readily effected. The different contrasting

zones of F 24 will be kept under further observation, but there is every reason to believe that after a few years the differences will have disappeared (cf. p. 365).

Elgee (8, p. 8), dealing with the heath association of Eastern Yorkshire, comes to the conclusion that the effects of burning depend on whether the fire has been with or against the wind. In this connection I should like to quote a few sentences from a letter written to me by Mr W. C. Marshall (at the time Chairman of the Local Committee); he says: "I have no doubt fires must always travel with the wind, though of course if the wind is slight and the fires are started in very dry stuff they will go up wind to some small extent. The tendency is to spread out in a fan shape. Anyone however standing in front of the fire will feel when the fire gets close to him strong gusts coming from the opposite direction, caused by the inrush of air to take the place of the hot air ascending from the fire. A large fire causes very considerable local disturbance of this sort and gives the impression that it is advancing against the wind when it is not."

Zone 2 on the central ridge included a considerable number of scattered trees, many of them of quite appreciable height, so that in spite of the intensity of the fire it had failed to reach the tops which were nearly all green in July 1924, although the branches on the lower parts were mostly dead¹. Judging by the development of the leaves on the upper branches, however, the conducting system in the main trunk cannot have been seriously impaired by the fire. Many of the burnt trees were sprouting from the base, viz. *Betula pubescens*, *Ilex aquifolium*, *Pyrus aria*, *P. aucuparia*, *Rhamnus frangula*, but *Pinus sylvestris* does not show this phenomenon. Some of the birches that had been completely burnt were sprouting not only from the base, but at various points up the trunks to near the top of the tree (cf. 7, p. 289); this, though a rare phenomenon, has also been noted on other burnt areas where too a similar sprouting from some of the thicker branches was observed. It is evident that the birch has a considerable capacity for the formation of such adventitious branches, since on the gravel areas in valley B some of the younger birch trees have been found sprouting from the base, although quite healthy above.

Another method of rejuvenation was noted in the case of *Pyrus aucuparia*, which apart from sprouting from the base of the main trunk, also puts out new shoots from its horizontal roots. These shoots may arise at a distance of 5-6 ft. away from the main trunk.

5. OBSERVATIONS ON THE LATER PHASES OF RECOLONISATION.

Some years after a fire the vegetation on a burnt area closes up and, viewed from a distance, appears continuous. On closer inspection, however, one always finds more or less numerous bare charred patches which may reach a yard or more in diameter, though usually much smaller (from a few inches to a foot

¹ Many of these trees have since been removed.

broad); in most cases they are larger and more numerous on the upper than on the lower parts of a slope. These patches are usually occupied by small mosses (mainly *Ceratodon*) and especially by species of *Cladonia*, which appear to remain sterile as long as the surrounding growth is low, but later fruit plentifully; practically all the species listed on 2, p. 134, occur, except for *C. sylvatica*. The origin of these bare patches is still obscure. In many cases they contain the burnt remains of a former *Calluna* plant, whose white bleached stems persist for many years after a fire. The size of the stems shows that they must have belonged to tall plants and it is possible that the heat generated when they were burnt has deleteriously altered the character of the soil in their vicinity. The few soil determinations that have been made (4, p. 67) are not adequate to establish this point, though hinting at some differences between the bare patches and the adjacent clothed areas. By no means all the bare areas, however, give such indications of former growth and it is probable that some of them were already bare prior to the last fire.

The general Phanerogamic succession previously given (2, p. 137) and gleaned from a comparison of burnt areas of different ages, has been corroborated by observations made on one and the same area at successive periods¹. There is, however, one important deviation noted on practically all the slopes with a south aspect, most strikingly on the *Erica* slope. This is the dominance of *Erica cinerea* in the C U E phase to which attention was drawn in the first contribution dealing with the Hindhead heath (1, p. 154) and which was there described as being a prominent feature of the heaths of this part of Surrey. Comparative observations made in 1921 and 1922 have afforded some facts towards the elucidation of this phenomenon. Slopes with a southerly aspect will be more exposed to solar radiation and are also specially affected by the prevalent south-west winds. In July of 1921, after a very hot spell, a large number of the young *Calluna* plants and seedlings on the slopes with a south aspect were brown and dead, while *Erica cinerea* was far less affected, most of the young plants looking quite thriving. This heavy mortality of the *Calluna* plants was noted on the *Erica* slope, on F 12, on F 13, and on F 20, but not on F 11 with a W.N.W. aspect. Moreover, on the lower parts of the slopes where the surrounding growth is taller (cf. p. 367) and there is more shelter, the mortality of the *Calluna* was not nearly as marked as on the upper parts of the slopes; this is especially true in the *Molinia* zones, such as that at the base of the *Erica* slope. A further confirmation of the conclusion suggested by the above observations that the dying of the *Calluna* is a drought effect is afforded by the fact that in July 1922, after a very wet and cool season, no such mortality on the part of the *Calluna* plants was observed. It would thus seem that slopes with a southerly aspect (especially in dry hot summers) are not conducive to the thriving of the younger *Calluna* plants, whilst *Erica*

¹ In spite of long-continued observation, the only addition to the list of species given on pp. 133-4 of the 1915 paper is the occasional occurrence of *Ficaria verna* along the paths.

cinerea is not affected in the same way; as a result the latter attains to a more or less marked degree of dominance.

When a hot summer follows soon after a fire, i.e. during the early stages of colonisation, the *Erica* may attain a very marked degree of dominance, while in later stages the effect is not so pronounced because there are already a number of older *Calluna* plants which are not affected. Thus, the dominance of the *Erica* in 1921 was much more marked on F 20 than on F 16.

In July of 1921, and to a less extent during the subsequent three years, F 20 showed a very striking division into three zones, the boundary lines between which ran roughly at right angles to the path in valley A (Fig. 1). The most northerly of these three zones bore a rich growth of *Erica cinerea* in full flower, although closer inspection showed that there was a great deal of prostrate *Ulex nanus* as well. In the next zone there was little *Erica* and the *Ulex* was altogether dominant. In the third zone bracken, which was fairly abundant also in the first, was the dominant. The first zone (being part of F 11) had been occupied by relatively low growth, the other two zones by taller growth prior to the fire. In the first zone there was abundant sprouting *Erica cinerea*, which being in its second year was in full flower, whilst a large proportion of the *Calluna* as above described had been killed off by the drought. Zone 2 had little sprouting *Calluna* or *Erica cinerea* (cf. p. 362 above) and the *Ulex* was therefore dominant, whilst zone 3 was merely zone 2 plus dominant *Pteridium*. Here therefore there was a startling difference between adjacent vegetation zones that one might easily be tempted to ascribe to soil conditions, but which was a combined result of the diverse height of the vegetation burnt in F 20 and the hot summer of 1921. In 1926 it was quite impossible to distinguish zones 1 and 2 which, in the course of further development, had come to resemble one another completely. The contrast between zones 1 and 2 of F 20 in 1921 is paralleled by the contrast between zones 1 and 2 of F 24 in 1926 (cf. p. 362).

The cause of the dying of the *Calluna* and the survival of the *Erica* is however at present not altogether explicable. The former roots more deeply as a general rule than the latter (2, p. 120) and Dr Haines informs me that the drought resistivity of *Calluna* plants is considerably greater than that of *Erica cinerea*. It must be remembered however that both these observations refer to the mature plants and, as regards the latter feature, no data are at present available respecting the young ones¹. The rooting depths of the young plants appear to be about the same. One significant observation may however be mentioned in this connection. On dry windy days, even in a wet summer, the growing tips of the younger *Calluna* plants, on the exposed upper parts of the common, are in large part limp and almost drooping, which is a first symptom of wilting with these forms. None of the other heath plants show this phenomenon, nor do the older *Calluna* plants often exhibit it. It is far less evident

¹ Dr Haines however tells me that the drought resistivity of *Calluna* increases greatly with age.

after rainy weather, although apparently not disappearing altogether. It seems very probable that it implies a lesser capacity on the part of young *Calluna* plants to absorb moisture and that this is responsible for their death in a hot dry summer. A curious feature of this bending over of the tips is that the curvature is nearly always away from the direction of the prevailing winds. It is probable that a careful examination of the root systems of young plants of *Calluna* and *Erica* would throw light on the phenomenon just discussed.

6. THE INFLUENCE OF EXPOSURE ON THE LATER PHASES OF THE DEVELOPMENT OF THE HEATH (INCLUDING GROWTH FORMS).

A considerable number of observations on the effect of exposure on the vegetation of the heath have already been contributed (1, p. 161; 2, p. 122). A very striking outcome of this factor is the change in the height of vegetation of equivalent age, as one passes from the tops down the slopes into the valleys.

Table II. *Average maximum heights¹ of different members of the heath vegetation at different levels (heights in centimetres).*

Locality	Plant	1921			1922			1923		
		Top	Middle	Bottom	Top	Middle	Bottom	Top	Middle	Bottom
F 16	<i>Ulex nanus</i> ^a	45.5	58.5	78.5	45.5	62.5	84	51	57	73.5
	<i>Calluna</i>	42	68.5	61	43	53.5	63.5	51	65	66
	<i>Erica cin.</i>	30.5	37	40.5	33	42	48.5	38	43	45.5
	<i>Pteridium</i>	51	71	—	44.5	56	73.5	48.5	63.5	76
F 16a	<i>Ulex nanus</i> ^a	63.5	56	66	63.5	51	75	—	—	—
	<i>Calluna</i>	43	58.5	71	51	56	68.5	—	—	—
	<i>Erica cin.</i>	32	37	38	35.5	38	43	—	—	—
	<i>Pteridium</i>	75	68.5	99.5	68.5	58.5	77.5	—	—	—
	<i>Ulex europ.</i>	130	—	150.5	150.5	—	153	—	—	—
F 11	<i>Ulex nanus</i> ^a	43	42	70	38	43	66	—	—	—
	<i>Calluna</i>	44.5	66	—	48.5	63.5	—	—	—	—
	<i>Erica cin.</i>	32	48.5	—	37	51	—	—	—	—
	<i>Pteridium</i>	54.5	68.5	106	44.5	67.5	82.5	—	—	—
	<i>Ulex europ.</i>	—	—	181	—	—	194	—	—	—
	<i>Erica tetralix</i>	37	54.5	—	38	53.5	—	—	—	—
F 12	<i>Ulex nanus</i> ^a	56	—	66	51	—	63.5	—	—	—
	<i>Calluna</i>	61	—	63.5	56	—	63.5	—	—	—
	<i>Erica cin.</i>	45.5	—	48.5	43	—	52	—	—	—
	<i>Pteridium</i>	71	—	73.6	57	—	62.5	—	—	—
	<i>Ulex europ.</i>	—	—	173	—	—	173	—	—	—

¹ Each based usually on about a dozen measurements.

^a Projecting upright shoots.

This is well illustrated by Table II. The measurements here given indicate the average heights of outstanding specimens at the different levels, the general level of the vegetation being in each case somewhat lower (especially at the tops); the *Pteridium* fronds of course stand higher than the other constituents of the flora. The vegetation on the tops shows a much more uniform level than that on the slopes, even than that on the upper parts of the slopes. On the tops every projecting tip, as observation shows, is liable to desiccation

(2, p. 127) and this keeps the general level uniform, while on the slopes where mutual protection comes less into play the more robust members grow more rapidly than the others and we get diversity of level. This is very strikingly shown by *Ulex nanus* (2, p. 126), which forms few upright projecting shoots at the tops but quite a considerable number on the upper parts of the slopes, although these are never as tall as at the bases of the slopes (cf. Table II). Where, however, protection is afforded at the tops (as by the abundant tall *Ulex europaeus* at the summit of F 16a) the plants may grow as tall as at the bottoms of the slopes.

Table III. *Measurements of individual plants at successive levels up the slope of F 11 in July 1922 (cm.).*

Position	Calluna	Erica cinerea
(a) Up to 50 ft. above the base line	89, 85.5, 73.5, 89, 76.5, 71, 70, 76.5	58.5, 67.5, 53.5, 47, 58.5, 73.5, 56, 57.5
(b) Between 50 and 100 ft. above the base line	54.5, 62, 57.5, 63.5, 58.5, 61, 59.5	48.5, 45.5, 43, 48.5, 53.5, 47, 43, 48.5
(c) Between 100 and 150 ft. above the base line	54.5, 51, 40.5, 45.5, 51, 56, 56	35.5, 48.5, 40.5, 40.5
(d) Above 150 ft. above the base line	49.5, 54.5, 45.5, 52, 48.5, 42, 43, 45.5, 38	38, 39.5, 34.5, 42, 45.5, 33, 39.5, 30.5, 35.5, 34.5, 30.5, 33, 35.5

The difference of height¹, as between the tops and the valleys, is always very striking and may be so marked that one would be inclined to suspect different fire zones, were it not for the fact that the change of height is quite gradual. Table III is given in illustration of this point and requires no further comment. The very striking difference in height² is no doubt conditioned in part by the greater water content and usually greater humus content of the valleys and lower parts of the slopes as compared with the tops (4, p. 56), but the varying degree of exposure to wind is certainly also a potent factor. This is shown by many observations, to wit the more frequent dying away of the tips of exposed plants at the tops, the greater abundance and larger size of the bare areas at the tops, and the actual physical data that have been obtained (2, p. 124). As regards the fronds of *Pteridium*, the effect of shelter was well shown on F 22 in 1922; the average height of the fronds at the base of the slope was 38 cm., whilst those growing in the shelter of a mass of dead *Ulex europaeus* near by averaged 85 cm.

The gradual disappearance of the sharply defined fire boundaries, referred to at the commencement of this communication, is probably likewise a result of shelter. Thus for many years the boundary of F 11 stood out sharply from afar, but in 1922 it was becoming very difficult to recognise and could not be

¹ It is noticeable that the cushions of *Ulex nanus* are flat and broad near the tops, but tend to be much more convex lower down the slopes.

² Associated with it are marked differences in habit and anatomical construction of the respective plants, features that will shortly be dealt with by Miss N. E. Bright of this department.

seen at all, when one was close at hand. It is the favoured growth of the plants at the edge of such a burnt area, due to the shelter afforded by the adjacent taller growth, that gradually leads to the blurring of the boundary line.

There is undoubtedly a very great tendency for the tips of exposed plants to die away. The majority of the *Pinus* plants colonising the gravel areas on the western slopes of valley *B* exhibit dead tips to the main axes and often to some of the laterals as well; many of these are too far above the ground to be caused by rabbit nibbling, moreover in many cases one still finds the dead tip, though shrivelled and brown. Plants that are well sheltered do not show this phenomenon. In July 1921 a considerable number of the *Ulex nanus* plants near the top of the *Erica* slope had upright shoots projecting well above the general level; all of these without exception showed dead tips having dried out to some little distance below the apex. Below the latter arose a group of laterals, each terminating in a spine, which at this time usually appeared fresh and green, though some of them were already turning brown. The death of projecting tips of *Calluna* has already previously been commented upon (1, p. 153).

Calluna, like *Ulex*, exhibits different growth forms which are probably largely the result of diverse response to exposure. Most successful are the bushy forms in which several, and often a considerable number of, branches arise from the base of the plant. Such generally show few dead branches and small leafy shoots occur in profusion on the upper parts of the plant. A contrast is afforded by individuals in which there is a prominent tall main stem bearing only dead branches below, but more or less abundant leafy ones above. Such plants, as they get older, commonly become lanky, developing fewer and fewer leafy branches, many of which gradually die away, so that ultimately the greater part of the shoot system may be dead. This was the condition of many of the *Calluna* plants in the C U facies on the top of the central ridge prior to the fire of 1924. Not uncommonly such plants rejuvenate, even without the occurrence of a fire, by sprouting abundantly from the base or even from the lower parts of the thicker stems.

It is probable that the bushy growth form of *Calluna* results either from the upgrowth of a number of branches from the dense cushion that is often formed when a burnt plant sprouts or by the (perhaps repeated) dying away of the tip of a seedling plant as a result of wind trimming. It is to be noticed that, in the case of *Calluna*, sprouting plants always form upright shoots sooner or later, whilst in the case of *Ulex nanus* this is by no means the case, only occasional ones doing so. This is probably a question of vigour. It is noticeable moreover that when a *Ulex nanus* plant forms a number of upright shoots, these generally look thoroughly healthy, whilst when only one or two are formed they generally die away very soon. Flowering takes place much more freely on the upright than on the prostrate shoots of this plant.

In July 1922 a considerable number of *Calluna* plants were collected from

different burnt areas in order to determine, by counting the number of annual rings, the probable date of the respective fires. In all cases the extreme base of the stem was sectioned, but the result showed the plants on a given piece of ground to vary somewhat in age. This one would expect from the fact that some plants arise by sprouting from old stools, whilst others have originated from seedlings which moreover do not all grow at the same time. Somewhat more surprising was the fact that the plants often exhibited a progressive increase in age in passing down the slopes (cf. Table IV); it is to be noticed too that *Ulex nanus* does not afford the same result. The explanation is probably to be found in the fact that on the upper slopes the greater exposure leads to a successive dying away of the upright shoot system of the *Calluna* plants until sufficient shelter has been created for a permanent shoot system to establish itself. It will be noticed that on F 16a, which does not face the prevailing winds, this feature is very little pronounced. The results again indicate the great susceptibility of young *Calluna* plants to the effects of exposure.

Table IV. *Numbers of annual rings in plants of Calluna and of Ulex nanus on different burnt areas in 1922.*

Locality	Calluna	Ulex nanus
F 11, top	7-8	—
F 11, upper part	8-9	—
F 11, middle	9-11	—
F 07, valley A	12-15	—
F 16, top	3-4	3-4
F 16, middle	5-6	3-4
F 16, base	6-7	3-5
F 16a, top	5	3-4
F 16a, middle	6	3-4
F 16a, base	5-6	4

The different growth forms of *Ulex europaeus* (3, p. 31) and *U. nanus* (2, p. 125) have in general already been fully considered. Miss Skipper, in the case of the former, distinguished between "ordinary" and "ericoid" types, the former differing from the latter *inter alia* in the possession of a more robust habit with long stout primary spines. No definite relation between these two growth forms and habitat conditions has, however, so far been established. It would seem that two similar types can also be distinguished in the case of *Ulex nanus*. The tall specimens (1, p. 151; 2, p. 127) found at the bases of the slopes have short spines and exhibit an "ericoid" habit, while the type with more robust spines is found principally on the upper parts of the slopes. This distribution is not, however, found everywhere on the common, and the two types, as in the case of *U. europaeus*, are connected by transitional forms.

7. THE EFFECT OF REPEATED FIRES ON THE SAME PIECE OF GROUND.

Haines (4, p. 69) has shown that fires lead to the destruction of 60 per cent. of the original humus when relatively young heath is burnt, but only about 30 per cent. in the case of older heath. Fires at frequent intervals will therefore

lead to a progressive reduction in humus (and also in salts), which appears to make conditions of life easier for plants that do not belong to the regular heath flora on this common and in particular, where bracken is lacking, to encourage the growth of mosses and grasses. The area F 22 on the eastern slopes of valley *B* has frequently been invaded by fires during the period of observation. While no detailed survey has been undertaken in this region, occasional records made from time to time tend to show that the true heath flora is here gradually diminishing in importance. In May 1924, two years after the last fire, when in most cases the new vegetation would be commencing to close up, a very large part of the ground was covered with mosses (*Polytrichum piliferum*, *Ceratodon purpureum*), *Ceratodon* giving a very noticeable brownish coloration to the surface, when seen from afar; lichens on the other hand were very scanty. Grasses of various kinds, mainly *Molinia* and *Aira*, were frequent and there were a number of specimens of shrubby forms (incl. *Rubus*). In 1926, however, although considerable parts of the ground still remained open and covered by mosses, the true heath forms had again begun to assert themselves at most points, and the character of the vegetation was approaching more nearly to that found elsewhere. It is probable however that, if another fire occurs in the near future, the ericaceous forms will have a still harder struggle to appropriate the ground.

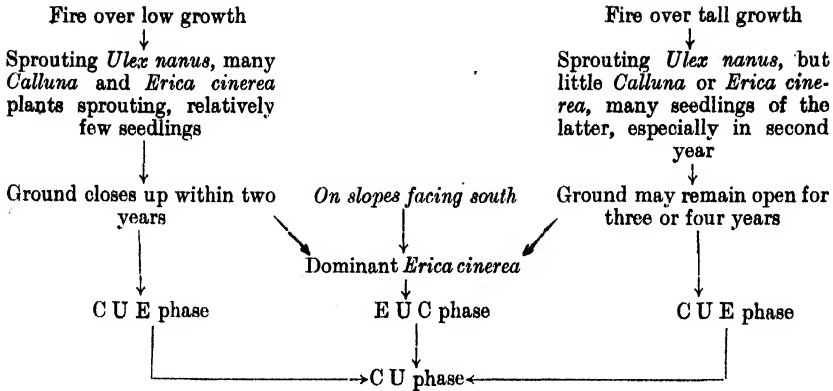
At the top of F 16a there is an extensive region, characterised by the absence of *Calluna*, the rather dense vegetation consisting of bracken, prostrate *Ulex nanus*, *Erica cinerea*, and great quantities of *Aira flexuosa*. It is thought probable that this represents a region frequently burnt in the past, with resulting dominance of the grass. It would seem that *Calluna* is more easily ousted than *Erica cinerea*, whilst *Ulex nanus* is the most tenacious of all.

No doubt the rapidity of degeneration of frequently burnt ground will depend on the readiness of access of grasses and of the casuals which replace the normal heath flora. It may be expected to occur more rapidly in the neighbourhood of highways than elsewhere. It is suggested that the type of vegetation encountered on many of the surrounding commons lying near the main roads—with an abundance of gorse, brambles, *Crataegus*, etc., as well as of various grasses and only occasional small patches of ericaceous forms—is primarily a result of frequent fires and progressive destruction of the humus.

8. GENERAL SUMMARY.

The general succession after fires on such a heathland as that on Hindhead Common and many adjacent parts of Surrey may be briefly indicated by the scheme on p. 371.

It appears that, except in the case of ground frequently burnt (see section 7), the vegetation always ultimately passes over to the C U phase, in which *Calluna* is completely dominant and by its tall growth more or less completely hides the codominant, but largely prostrate, *Ulex nanus*. There is no evidence that



the latter is in any way deleteriously affected by the dense shade cast by the *Calluna* which is probably largely responsible for the elimination of other forms. As previously pointed out (2, p. 137), spontaneous colonisation by *Pinus*, *Betula*, etc., would no doubt ultimately lead to the development of woodland, but over most parts of the common the trees are felled after they have reached a certain size.

The results communicated in the second section of this paper tend to emphasise the stationary character of such heath vegetation. Fires cause little ultimate change and, after a number of years have elapsed, the heath presents the same appearance and detailed composition as before. Its essential components are *Calluna*, *Erica cinerea*, and *Ulex nanus*, and all the others (*Pteridium*, *Vaccinium Myrtillus*, *Erica tetralix*, *Molinia coerulea*, *Aira flexuosa*), though frequently abundant, are locally absent over considerable stretches of ground. Evidence has been produced in the second and third sections which testifies to a spread of *Pteridium* and *Molinia* in the first years after a fire from regions (commonly the valleys) in which they were previously abundant, but such spread no longer occurs when the vegetation has closed up and the ericaceous forms have asserted themselves. Neither of these plants has, however, appreciably extended its domain during the sixteen years that the common has been under observation. Although rabbits occur plentifully on many parts of the common and evidently attack many of the plants present, there is no evidence that the biotic factor plays any considerable rôle in this region.

Apart from fires, varying exposure is the most important factor affecting the character of the vegetation. Growth in the valleys is more rapid and denser than on the tops, where the full effects of exposure are felt, but the change is quite gradual and this factor does not condition any sharp boundary lines.

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THE RESULTS OF AN UNINTENTIONAL ECOLOGICAL EXPERIMENT

BY V. S. SUMMERHAYES AND W. B. TURRILL.

RICHMOND PARK, Surrey, the largest of the parks open to the public in the metropolitan area, consists of undulating ground partly wooded and partly grassland. The underlying stratum is London clay, locally covered with younger sands and gravels of alluvial origin. The grassland has been much altered by grazing (by cattle, sheep, and deer) and treading, while certain parts are used for football during the winter months. On the northern side near Sheen Gate the normal semi-natural vegetation is of a slightly acid type in which *Holcus mollis*, *Festuca rubra*, *Galium saxatile*, *Potentilla erecta*, *Luzula campestris*, *Rumex acetosella*, *Veronica officinalis*, and *Agrostis* spp. are the chief constituents. *Holcus* locally forms almost pure societies, while in some places the grassland is replaced by bracken communities.

While walking casually over this part of the park in the spring of this year we noticed that in certain places narrow strips of vegetation differed from the normal. In other places vegetation was almost entirely lacking along certain lines, and investigation showed that these strips or lines corresponded with the touch-lines of various football pitches. Closer examination revealed striking alterations in the flora as a result of the presence of chalk or lime¹ added in marking out these touch-lines and it was thought that our observations were of sufficient interest to record. We treat separately two areas, one on higher ground, the other on lower, since it was found that the modifications of the vegetation resulting from the marking were slightly different in these areas, the differences probably being correlated with dissimilar water contents of the soil.

Higher ground. The locality where our observations were made lies just west of the Sheen Gate and consists of almost flat ground with no obvious superficial drainage. The turf here is very short and in places rather sparse and is traversed by numerous, parallel and closely adjacent, or sometimes intersecting altered strips of vegetation representing the touch-lines of successive years. The first result of the deposition of the chalk or lime, especially where much was deposited, is the almost complete extermination of the vegetation. Scattered plants of some of the species may survive of which the most prominent is *Cynosurus cristatus* which occurs on the pitches in small quantity and is possibly a relic of seed-sowing in past years. Where the

¹ The exact composition of the white marking material when first applied varies. It is sometimes made of slaked (slacked) lime, sometimes of unslaked lime, and sometimes of whitening. The first is rarely completely slaked and causes some "burning" which is very marked when unslaked lime is used.

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marker had been emptied circular patches are found about a foot in diameter and these are perfectly devoid of vegetation. After the initial destructive effect of the marking material the conditions gradually improve owing to dilution and washing into the soil by rain, and the bare or partially denuded strips are invaded by species which ordinarily do not maintain themselves in quantity in competition with the normal vegetation. Such plants are *Cynosurus cristatus*, *Lolium perenne* and *Trifolium repens*. By degrees the lines become completely colonised by these species associated with a few individuals of the surrounding grass-heath flora. At this stage the lines are easily distinguished from the rest of the turf by the numerous inflorescences of *Cynosurus* and *Lolium*, these being very scattered elsewhere. The light yellowish green leaves and spikes of the former grass contrast strikingly with the surrounding greyish green *Holcus* which rarely occurs on the lines. On the other hand, *Rumex acetosella*, which flowers freely in the normal grasslands, also occurs in the strips but was not found in flower. Another difference between the lines and the unchanged grass-heath is the reduction of undecomposed organic debris lying on the surface of the former, this being undoubtedly due to the increased activity in the less acid soil of the bacteria which break down the debris. With advancing age the effect of the deposited material disappears and the adventives associated with it are replaced by grass-heath vegetation, but it is many years before the reversion to the original community is complete.

A series of soil samples was taken with the object of seeing what difference in soil acidity had been produced by the addition of chalk or lime. Samples taken around the roots of *Holcus* and *Galium saxatile*, about 1 m. from a typical line, gave pH values of 6.6 to 6.9. A corresponding sample of soil from the strip itself, the chief plant in this case being *Cynosurus*, had a pH of 7.4. A third sample from a near-by line quite recently marked and still white gave an even more alkaline reaction, viz. pH 7.8. These figures illustrate sufficiently the alterations in soil acidity consequent on the addition of the marking material and the subsequent leaching.

Lower ground. The second locality was near the Beverley Brook, a short distance from the Roehampton Gate. Here the substratum is considerably damper, *Juncus effusus* being found abundantly near the brook and occurring in scattered tufts on the pitches themselves. The grass-heath in this region is composed predominantly of *Festuca rubra*¹, which forms small tussocks, together with *Luzula campestris* and abundant *Galium saxatile*, the whole having a dull brownish green tinge at the time of our visits.

The first effect of the chalk or lime seems to be the same as on the higher ground but, owing to the greater water-content, invasion of the more or less denuded strip takes place more rapidly. The chief species occurring here as

¹ Series of specimens of the *Festuca* were submitted to Mr W. O. Howarth who kindly reports that they are *F. rubra* L. subsp. *genuina* (Hack.) var. *vulgaris* Hack. and intermediate between subvar. *vulgaris* Hack. and subvar. *barbata* Hack. There is a considerable range in the degree of hairiness of the glumes in different plants.

first invaders are *Poa annua* and *Trifolium repens*, the two imparting to the lines a deep rich green coloration. Other species found less frequently include *Rumex acetosella* (sterile), *Achillea millefolium*, *Cerastium vulgatum*, *Carex goodenovii*, *Lolium perenne* and *Galium verum*. A striking feature of the lines in this district is the abundance of worm casts, especially noticeable after rain, these being almost entirely absent from the surrounding unmarked grassland. Where slight hummocks occurred in the course of the line it was noticed that there were breaks in the strip of modified vegetation and here normal grass-heath appeared unchanged. Whether these were due to the tilting of the machine preventing efficient deposition of marking material, or whether the chalk or lime deposited had been leached rapidly from these hummocks, could not be ascertained. As on the higher ground a marked difference in the organic litter lying on the ground was noticeable, there being practically none along the lines, whereas on the surrounding turf a thin brown layer was everywhere visible. It is worth noting that the deer, of which there are a considerable number in the park, found the *Poa* much more palatable than the *Festuca*, for while the former in places had been nibbled quite short, the latter seemed almost untouched.

At a later stage an interesting contrast is afforded by the distribution of the two species of *Galium*, *G. verum* and *G. saxatile*. The latter grows abundantly right to the edge of the affected strip where it ceases quite abruptly and is there replaced by its congener, reappearing with the same abruptness on the other side. With the gradual disappearance of the chalk and lime effects *G. saxatile*, however, re-invades the strips together with the other members of the normal grass-heath flora. From our observations it seems probable that the whole process of succession is completed in a shorter time than on the higher and drier ground.

While the observations recorded above are by themselves of no great importance yet they may be of use to others engaged on similar communities in districts not so much affected by man's activities. It would also be of interest to compare data of a similar nature collected from districts where the soils and plant covering are different from those of Richmond Park.

SCHEME FOR ABSTRACTING PUBLICATIONS ON BRITISH EMPIRE VEGETATION

(BRITISH EMPIRE VEGETATION COMMITTEE)

THE BRITISH EMPIRE VEGETATION COMMITTEE (appointed by the Imperial Botanical Conference held in London in 1924), which last year completed the preparation and publication of *Aims and Methods in the Study of Vegetation*, thus carrying out Resolution 10 of the Conference, now desires to put into effect Resolution 9 of the Conference—that all future work published on the vegetation of the Dominions and Colonies should be registered and abstracted, the abstracts being made generally available by periodical publication.

The plan proposed is to invite authors of papers and books throughout the Overseas Empire dealing directly with Vegetation and Ecology in its widest sense and also with other publications likely to be of use to students of these subjects to send to the Secretary of the Committee (Dr T. F. Chipp, 199 Kew Road, Kew, Surrey) abstracts of their publications. In the case of books or papers dealing directly with vegetation and ecology, or as a whole of direct interest to ecologists, the abstracts should be of the type customarily given at the conclusion of papers in scientific journals, and should not as a rule exceed 3 to 5 per cent. of the length of the paper. Very often they may be much shorter than this, though in the case of papers describing new and important results of thorough ecological or vegetational work they may have to be longer. Many papers and books not dealing *directly* with ecology or vegetation, but of the existence and nature of which it is desirable that ecologists should be aware, such as floras, floristic lists, work on climate, geology, soils, agriculture, forestry, etc., may be adequately noticed in a very brief space, sometimes in a line or two, or may be merely cited in title where this is sufficiently descriptive. When certain parts only of a publication are of ecological interest, such parts only should be abstracted.

When a separate copy of the publication can be conveniently sent with the abstract this should be done.

The abstracts will be collected and edited by a number of collaborators, each dealing with a specific portion of the Overseas Empire, and will then be published, by arrangement with the British Ecological Society, in the form of supplements to *The Journal of Ecology*. Each collaborator will see that so far as possible all publications bearing on the vegetation and ecology of the part of the Empire for which he is responsible are abstracted, and will himself deal with publications of which he has not received abstracts.

The supplements containing the abstracts will be published as soon as enough material has accumulated, and, it is hoped, will in the future accompany

each issue of the *Journal*. There is, however, not yet enough material in hand to publish a supplement to the present issue. The supplements will be included in the subscription price of the *Journal* but will also be obtainable separately. The scheme will begin with publications bearing the date of 1927.

A circular describing the scheme in detail was distributed throughout the Empire in March last. Further copies may be obtained from Dr T. F. Chipp, Hon. Sec. of the British Empire Vegetation Committee, 199 Kew Road, Kew, Surrey.

"TRANSPLANT COMMITTEE" OF THE BRITISH ECOLOGICAL SOCIETY

Appeal for Funds

As the result of a suggestion by the Director of Kew a Committee has been formed with the object of undertaking experiments on the effect of differing conditions on the form, structure and other characters of plants of identical genetic constitution. In the first instance it has been decided to experiment on six species, using only plants derived from genetically pure seed of known origin, and growing 25 specimens of each species on each of several different soils of selected types, side by side in the same garden. Mr E. Marsden Jones, of Potterne, Wilts, has very kindly undertaken to carry out these experiments for which most of the plant material is available. The necessary cost of obtaining and transporting the soils and of making the beds is however considerably in excess of £100. Part of this sum has already been collected but more is wanted, and individual members of the British Ecological Society are asked to contribute what they can. Subscriptions should be sent to Mr W. B. Turrill, Hon. Sec. of the Committee, The Herbarium, Royal Botanic Gardens, Kew, Surrey. Cheques and Postal Orders may be crossed "Transplant Committee Fund (c/o A. W. Hill), Barclays Bank Ltd., Kew Green Branch."

Information on the progress and results of these experiments will be published in the *Journal* as it becomes available.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

Allorge, P. and Denis, M. "Notes sur les complexes végétaux des lacs-tourbières de l'Aubrac." *Arch. de Bot.* 1, 2, pp. 17-36, 2 figures in the text. 1927.

The Aubrac region is part of the central volcanic "massif" of France. It lies south of Cantal in the angle between the rivers Lot and Truyère. The plateau, which is approximately 1500 m. in height, is built of granite and basalt. The rainfall is high, 1000 to 2000 mm., with much snow in winter. These conditions, with a humid climate, result in beech forest as the natural climax where drainage is good. This beech forest is of the same type as that in the Cevennes. At the present time, however, it only remains in fragments. Where the drainage is poor there are found lakes, swamps, and land liable to floods. These occur especially on the north-eastern part of the plateau and are the portions especially studied.

Four lakes occur, the largest having an area of 11 hectares and a depth of 11 m. The margins of the lakes usually rest on fluvio-glacial deposits or peat, and the lakes are surrounded by swamps. The junction between lake and swamp is a fluctuating one. Of the aquatic associations in these lakes the plankton is poor in species and not characteristic. It is intermediate in type between that of western and that of central Europe. The submerged leaf type, *Myriophyllum alterniflorum*, is also poorly developed and local. The *Nuphar* is more common, but contains few species. The *Isoetes echinosporae* is regarded as an association fragment. Of the characteristic species, *Isoetes lacustris* occurs on sands and is associated with *Littorella*, etc.: *I. echinospora* occurs on a peat bottom. The reed swamp is represented by *Scirpetum* and consists of social helophytes which occur in more or less pure groups rather than mixed.

The transition from aquatic to land conditions is represented by the *Caricetum filiformis* which builds up a substratum. This occurs in all the lakes and is a very varied community. *Carex filiformis* (*C. lasiocarpa*) alone is generally abundant.

Where the soil is aerated, this is followed by the *Juncetum silvatici*, an association dominated by *Juncus silvaticus*, with *Calamagrostis lanceolata* locally dominant. This association is considered to have relationships with the *Molinietum*, and contains several species that are regarded as characteristic of that. Development proceeds from the *Juncetum* to a *Salix* thicket or to *Agrostis* grassland. The community termed *Caricetum fuscae*, dominated by small species of *Carex*, is local in occurrence but succeeds to the *Caricetum filiformis* in patches.

Where the soil is saturated and not well aerated a different line of succession occurs. The *Caricetum limosae*, which contains few species, follows the *Caricetum filiformis*. This forms a floating mass difficult to enter. When the substratum gets firmer this is in turn followed by *Rhynchosporietum*, which itself is commonly followed by *Sphagnetum* with its characteristic and homogeneous flora. In time this is succeeded by *Calluna* and ultimately by *Betula*. Here the later stages of this succession are rarely allowed to develop. The destruction of the *Sphagnum* is brought about by *Polytrichum strictum* or by *Scirpus caespitosus*.

Lists of the principal species of each community are given. These lists are divided into "characteristic" and "accessory" species. Also under each there are added notes on the occurrence of the association in other places, and similarities or dissimilarities are noted.

R. S. A.

Shreve, Forrest. "The Vegetation of a Coastal Mountain Range." *Ecology*, 8, 1, pp. 27-44, 2 maps, 4 photos in text. 1927.

This is a general account of the distribution of the vegetation preliminary to detailed instrumental studies. The area is that of the Santa Lucia Mountains in California which form a range extending over 100 miles in length and 25-30 miles in width. The mountains rise to more than 3500 ft., the highest point being Junipero Serra Peak, 5844 ft. The slopes are

steep, the valleys without flat bottoms, and the vegetation dense with little continuous forest. The area has been little interfered with either for farming or lumbering. The climate has a winter rainfall and typically a dry rainless summer. The character of the vegetation is influenced by the proximity to the sea on the west and the relatively arid conditions on the east of the range. Altitude has little effect on the distribution; more important are slope, amount of soil, and prevalence of summer fogs. Very sharp local contrasts of vegetation are frequent.

Four vegetation types are recognised: *Hygrophytic Forest*, *Mesophytic Forest*, *Chaparral*, and *Grassland*. These represent a series of increasing dryness. The *Hygrophytic Forest* is generally dominated by *Sequoia sempervirens* often associated with *Lithocarpus densiflora*, and occurs in the larger canyons on the coastal slopes. In the largest canyons heavy pure stands or groves of redwoods extend 600–800 ft. up the slopes and to a distance of 6–8 miles from the sea. Isolated redwood groves occur near the sea up to 1500 ft. The redwoods cast a dense shade and the associated plants are of a hygrophytic type though less so than in the corresponding forest further north. The *Mesophytic Forest* never forms extensive pure woodlands but is very much diversified both in species and in the type of tree. While evergreen oaks are the most general dominants they are associated with a number of other trees including conifers (*Pinus*, etc.). The shrubs that occur here are those associated with the moister parts of the Chaparral. *Chaparral* occupies more than half the area. It is exceedingly varied in composition in different portions. The features of several types are described. *Grassland*, which is only active in the spring and passes most of the year in a dormant state, is regarded as the most xerophytic type. Grasslands occur on soils about 1–2 ft. in depth. On the ocean side grassland is frequent on rounded wind swept ridges. The distribution of these types in a limited portion is described and a map of this area is given.

R. S. A.

Kelley, A. P. "Dune Formation by Pine Barren Plants." *Bot. Gaz.* 83, pp. 89–93, 2 photos in text. 1927.

The Pine Barren region of southern New Jersey is an extensive system of sand dunes covered for the most part by forest, largely composed of pines. The forest floor has a fairly complete covering of vegetation. Wherever a plant dies the sand becomes exposed and is very easily removed by wind. A hollow is scooped out, the sand carried away, and ultimately deposited against some protruding object. The pine trees on the sand hills produce basal whorls of branches that tend to accumulate sand. The branches get buried by sand but the tips continue upward growth. Growth in these branches continues even after the main tree dies, and a sand hill is produced. In addition to such isolated sand hills, long dunes are formed, especially at the junction of the pine and oak forests. The sand drifts through the rather open pine forest but is stopped by the closer growth of the oak forest. In the Pine Barren region dune movements are rather slow and the pines can in most cases keep pace with them.

R. S. A.

Tharp, B. C. "Structure of Texas Vegetation East of the 98th Meridian." *Univ. Texas Bull.* No. 2606, pp. 97, 30 plates. 1926.

This is an extensive study of the vegetation of the eastern part of the State of Texas. The area covered represents about 80,000 square miles. After a general discussion of the work of previous investigators, a short account follows of the climatic, geological, and topographic features. The greatest precipitation occurs in the south-east. The land rises from the coast to a height of 1000 ft. in the north-west part of the area. The various geological formations outcrop roughly parallel to the coastline.

The classification of the vegetation and the terminology follow the scheme of Clements. The term "society" is used mainly to designate the layers, though aspect societies are also recognised. Four formations are distinguished, *Southern Evergreen Forest*, *Deciduous Forest*, *Prairie Grassland*, and *Mesquite Woodland*.

The first of these occupies the largest area and the region of most precipitation and moisture. The dominating tree here is *Pinus palustris*, associated with *P. taeda* in the southern

parts, and with *P. echinata* in the northern. A description and list of the climax is given. In this part a hydrosere is traced up to a hardwood forest through *Taxodium* swamp. The relation of this forest to the climax pine forest is discussed. Pines do not appear to invade till the streams cut down so far that drainage occurs. The *Taxodium*-hardwood forest is looked upon as an edaphic subclimax. The pine forests have been very much reduced in extent at the hands of the lumberman. The cut areas are especially liable to fire, and under such conditions the pines reproduce very slowly. Frequently the ground becomes occupied by thickets of dicotyledonous shrubs that occur as accessory species in the climax. Pine regeneration takes place readily when fire is prevented, especially if seed trees are left.

The Deciduous Forest always occurs on sands on the higher ground further inland than the pine forest. *Quercus stellata* is the general dominant though often associated with *Q. marylandica* and *Carya buckleyi*. This forest is of rather limited extent. When the forest is cut regeneration by coppice occurs freely. Where cutting is followed by intensive grazing grassland becomes established, but as soon as conditions allow the forest regenerates. There is a broad transition zone between these two types of forest, where a mixed Pine-Oak forest is developed which occupies larger areas than the deciduous forest.

Inland of the deciduous forest occurs the Prairie Grassland which is found on heavy black soils. This association has been much altered by grazing and cultivation and anything approaching a natural climax can only be found where protection has been afforded. In such spots *Andropogon saccharoides* and other species, with *Stipa leucotricha*, are the dominants. *Bulbilis dactyloides* and *Aristida* dominate in overgrazed parts.

Secondary successions have been traced in abandoned arable land. If undisturbed the climax is attained in about 25-30 years. The effects of grazing are described, also the invasions of woody plants. The prairie has a broad transition zone with the pine and deciduous forests where there are alternating areas of the two types.

The Oak-Cedar-Mesquite Woodland only occurs on the western limits of the area studied and is briefly described.

A large area, 10,000 square miles, of flat land along the coast is covered by grassland of rather varied composition. This coastal prairie extends from regions of 50 in. rainfall to those of 30 in. It is regarded as being composed of seral units, and invasions by woody plants of the bordering communities are described. The coastal marshes are closely associated with this prairie and shade off into it.

For each formation lists of the species occurring are given, subdivided according to the parts played by each of the plants. The account is illustrated by a large number of excellent photographs.

R. S. A.

Ostenfeld, C. H. "The Flora of Greenland and its Origin." *Det Kgl. Danske Vidensk. Selsk. Biol. Med.* 6, 3. 1926.

The flora of Greenland, at any rate as far as the vascular plants are concerned, has now been fairly well worked out. In this flora 390 species are known. In this estimate many of the species are somewhat aggregate Linnean species though in some genera smaller units are available. The distribution of these plants has now been worked out for the whole country along the coastal belt, the only part where flowering plants occur in any quantity. After a brief summary of previous work on the flora and of the theories that have been put forward as to its origin, the question of its age is discussed. At the present time flowering plants are found on rocky walls or ledges which are free from ice, known as "nunataks," even as far north as 81° N. Lat. The existence of these plants in conditions that are quite glacial, lends support to the view that some plants in the flora date from preglacial times. The number of these survivors is not large however, the great majority of the flora having come in since the period of maximum glaciation.

In the south and south-west of Greenland there were at one time Norse colonies of which remains exist. These settlements were occupied for 400-500 years up to about the middle of the fifteenth century. About 50 plants in the flora which are almost or quite confined to this region are regarded as owing their origin to the Norse colonists.

Greenland is divided into 15 divisions for purposes of plant distribution. The species are further divided according to their phytogeographical types; high arctic, arctic, and sub-arctic. They are also grouped according to their distribution outside Greenland. The results for the floras of each division are set out in a table. The analysis brings out very strongly the much more abundant flora on the west coast as compared with that on the east. Several

causes contribute to this: the conditions are less severe, the amount of ice-free land is greater, and the distance from adjacent lands is less. Also the Norse cultivation was confined to the west coast. Of 134 species that occur only on the west coast 50 are attributable to Norse origin. The east coast has only 9 peculiar species, two of these being European, the others Arctic. Two arctic American species are found on the east coast only, at the head of a fjord, and appear to have reached this spot by migration across the ice of the interior. The north of Greenland, beyond 76° N. Lat., has a poor flora, 125 species, of which 8 do not occur further south. Many species are stopped from reaching the north by the glaciers that extend to the sea. The various divisions exhibit different proportions of the various phytogeographic elements. Thus the percentage of high arctic species is at a maximum in the north and at a minimum in the south. Exactly the reverse occurs with the subarctic species. The arctic species attain their maximum on the coasts, falling off to the north and the south. At present there are eight endemic species known in Greenland, though further study of critical genera, *Taraxacum* and *Hieracium* for example, may lead to an increase in the numbers. Of the endemics two are very closely allied to species in arctic America, the others belong to genera with peculiar sexual reproduction. Four species of *Hieracium*, for example, belong to sections of the genus that are not found in arctic America but occur in Scandinavia. In Greenland these are almost wholly in the south-west and it is suggested that these plants are the descendants of plants brought in by the Norsemen, though the parent forms have disappeared.

The flora is considered in relation to the distribution of the species outside Greenland. Of the 390 species 113 or 29 per cent. are definitely of American origin, 74 or 19 per cent. European, while 52 per cent. are of uncertain origin. If the 50 plants due to the Norse cultivation are excluded, the percentages become—American 33 per cent., European 7 per cent. Of the species of uncertain origin most are probably of western origin, though about 62 may be glacial plants. The flora as a whole is therefore predominantly of American origin. The routes of migration are discussed and stress is laid on that from the north-west. This is considered as of special importance owing to the general distribution of the plants and to the short distance from other land. Evidence is available that in post-glacial times conditions of much greater warmth occurred which would have allowed of this route being used by plants that could not withstand the present conditions. Wind transport over ice is emphasised as an important method of access of the flora.

R. S. A.

NEW BOOKS RECEIVED

McDougall, W. B. *Plant Ecology*. $7\frac{3}{4} \times 5\frac{1}{4}$ in. Pp. viii + 17-326. With a frontispiece and 115 figures. London: Henry Kimpton, 263 High Holborn, 1927. Price 14s.

This is an attempt to provide an elementary text-book of plant ecology by an Assistant Professor of Botany in the University of Illinois, who is already known to plant ecologists by his work on mycorrhiza. The earlier chapters are devoted to the "ecology" of roots, stems, and leaves, and these contain much useful information intelligently and interestingly put. The anatomy of roots, as compared with that of stems and leaves, is rather neglected. There are several chapters on "symbiosis," a term used by the author in an unusually wide sense, and then qualified by adjectives—giving us, for example, "reciprocal nutritive disjunctive symbiosis." This does not seem a very convenient or advantageous usage. The "physical factors" are next dealt with, under the headings light (including some account of the work of Garner and Allard), heat, air, soil and water. The remainder of the book is mainly devoted to plant communities and succession, and the treatment of these is, on the whole, distinctly modern and good, though it suffers rather from vagueness and even some inconsistency in places, as a result of the author's endeavour to reconcile the points of view of different authorities. Thus he appears to adhere at first to Clements's view of vegetation as an organism with a development as definite as that of an individual organism, but further on he introduces Nichols's system, which does not fit very well. The chapter on the distribution of plant communities is much too short to be adequate. No useful account can possibly be written in the space allowed. Finally there is a short chapter on applied ecology, and an appendix (for the teacher) on laboratory and field work. Each chapter is followed by a short list of literature in which it is pleasant to find English work adequately recognised. On the whole the book represents a praiseworthy effort and should be useful to the elementary student.

Markgraf, Friedrich. *Kleines Praktikum der Vegetationskunde*. $8\frac{3}{4} \times 5\frac{3}{4}$ in. Pp. v + 64. With 31 illustrations. Berlin: Julius Springer, 1926.

This is an attractive little guide to the study of vegetation in the field based on the author's own investigations of north German plant communities, mostly woodlands, and illustrated by excellent and beautiful photographs. The sociological treatment is predominantly static, the association being compared with a species, the individuals of which differ in negligible particulars. Plant aggregations on heaps of earth by the roadside or in arable fields are not admitted as communities. The analysis of associations is made with the aid of quadrats and follows on the whole the Zürich methods, but the Swedish conceptions of "constants" and "minimal area" are used. The conception of the "synusia" is used for lower grades of community within the association, and beechwood, for instance, is considered an "association-group." A section is devoted to habitat, and instruments for investigating the factors are described. The importance of observing seasonal succession is emphasised and well illustrated by photographs, and a few of the more obvious cases of succession in the wider sense are touched upon.

Waksman, S. A. *Principles of Soil Microbiology*. $8\frac{1}{4} \times 5\frac{3}{4}$ in. Pp. xxviii + 897. With 19 plates including 154 figures. London: Baillière, Tindall and Cox, 8 Henrietta St, Covent Garden, 1927. Price 45s.

This is a bulky work by a leading authority on a subject which, though its growth has recently been very rapid, may still be considered as in its infancy. Like ecology in the large, soil microbiology depends for its development on the advance of a large number of specialised branches of knowledge—bacteriology, mycology, algology, protozoology, chemistry,

physical chemistry and biochemistry. It is also necessarily concerned with special technique required for the investigation of the soil flora and fauna, and indeed for the investigation of general soil chemistry and physics as well. The whole of these subjects have advanced very rapidly during the last quarter of a century—soil science as a modern branch of investigation may be said indeed to have come into existence during that time, though the fundamental work of Beijerinck goes back more than 40 years. Prof. Waksman's work is the largest general book on soil microbiology that has yet been published. It is very comprehensive, containing accounts of the numerous detailed researches of recent years (of which the book noticed immediately below is a good example) in every branch of the subject, and will be of the greatest value as a work of reference for students.

Sandon, H. *The Composition and Distribution of the Protozoan Fauna of the Soil.* $8\frac{3}{4} \times 5\frac{1}{2}$ in. Pp. xv + 237 with a series of charts showing the distribution of species in the soil samples examined. Edinburgh: Oliver and Boyd, Tweeddale Court, 1927. Price 15s.

For the purpose of this work 145 samples of soil distributed all over the world, including the arctic and antarctic regions were examined by inoculation into suitable culture media. In none were Protozoa entirely absent, and curiously enough the largest number of species was found in a richly manured soil from Greenland. Flagellata, Ciliata, Amoebae and testaceous Rhizopods were the groups of Protozoa represented.

The attempts at correlation of the number of species of soil Protozoa with geographical region, nature of habitat, total nitrogen, loss on ignition, hygroscopic water, and pH value, gave very little result. The most that can safely be said in the light of existing data is that Protozoa are on the whole most numerous in species where there is the greatest food supply and the greatest number of bacteria (their chief food) and therefore in soils which are highly cultivated, and that the testaceous Rhizopods, which are not correlated with bacteria, are specially characteristic of peaty soils.

Out of approximately 250 species of Protozoa known from the soil most are remarkably widely distributed and the commonest are absolutely ubiquitous. Most of these are also practically ubiquitous in fresh water and commonly found in water rich in organic matter, though some belong to the plankton of clear waters. But many forms equally common in these habitats are absent from soil and there are about 20 species only known from soil. Thus the protozoan community of the soil can scarcely be regarded as an accidental collection of the less highly specialised types (though this description would apply to many of its members) and must be considered as a community with distinct characteristics, though we cannot as yet describe its ecological requirements. Many however can tolerate and some perhaps prefer anaerobic conditions.

Most of the book consists of a systematic account of soil Protozoa.

Stapledon, R. G. and Hanley, J. A. *Grass Land, its Management and Improvement.* $7\frac{1}{2} \times 5$ in. Pp. 159. Oxford, at the Clarendon Press, 1927. Price 5s.

"Research bearing on several branches of grass land management is at present making great progress" (Preface). This little book is intended primarily for the farmer who is willing to avail himself of this progress and to use new knowledge to help him to conduct "what in effect must be a continuous and life-long experiment." The authors begin with a short chapter on Natural Types of British Grass Land, distinguishing the Fescue-Agrostis Pastures, well drained and not predominantly acidic, from the more acidic Nardus and Molinia types and from "Grazings dominated by non-gramineous herbage," namely, Heather, Cotton Grass, Deer Grass (*Scirpus caespitosus*) and Saltings. It may be thought that the Fescue-Agrostis type, as given here, is too wide, since it includes the shallow calcareous soils of the chalk and oolite in which species of Agrostis, though not absent, are neither dominant nor characteristic, as well as the great range of well-drained hill pastures or siliceous rocks most of which are distinctly acid in reaction (though not of course so acid as the Nardus and Molinia types) and in which species of Agrostis are always a prominent feature. "Semi-natural types," to which the second chapter is devoted, are defined as those which are

enclosed by fences, so as to restrict and concentrate grazing, without manuring, and it is pointed out that this at once alters the balance of the vegetation.

The remaining chapters are devoted to various means of improving grass land for hay or pasture, to temporary grass (leys), seed mixtures, and so on, including a useful chapter on the characteristics of the "chief herbage plants." The importance of mechanical treatment in improving poor grass land, especially such as "mats" readily, is well emphasised. The book is full of interesting ecological points, though the ecologist would desire a considerably fuller treatment than can be expected in a work designed especially for the farmer.

Gates, R. Ruggles. *A Botanist in the Amazon Valley.* $7\frac{1}{4} \times 5$ in. Pp. 203, with a sketch-map showing the author's route and 11 photographic plates. London: H. F. and G. Witherby, 326 High Holborn, W.C., 1927. Price 7s. 6d.

This is a pleasantly written account of the author's voyage in 1925 up the Amazon as far as Tefé, more than 1300 miles up river from Pará. He spent altogether six weeks on the Amazon and evidently used his time to very good advantage, showing an insatiable curiosity not only in the luxuriant vegetation but in the varied scenes of human life he encountered. Most of the book is devoted to a narrative of the journey, but at the end there are two chapters of short notes on the Palms (in which the Amazon region is extraordinarily rich), Lecythidaceae and Bombacaceae encountered by the writer, and an interesting concluding chapter on "The People," in which the author argues that the complex mixture of Portuguese, Indian and Negro blood shows evidence of blending of hair, skin, eye-colour and type of feature, but also of segregation. Thus one man had "half black" skin but entirely white man's features, another absolutely white skin, light brown eyes and brown hair with no kink, but unmistakably negroid lips, mouth and nose—clear evidence of independent segregations. But the complexities of character combinations observed can only be explained by more than one pair of allelomorphs often being involved in the production of a "character."

Nicholson, E. M. *How Birds live: a brief account of bird life in the light of modern observation.* $7\frac{1}{2} \times 5$ in. Pp. x + 139, with a coloured frontispiece. London: Williams and Norgate, Ltd., 14 Henrietta St, Covent Garden, W.C. 2, 1927. Price 3s. 6d.

This attractive and often amusing little book is a very serious contribution to the ecology of birds. It deals with the means by which the bird population is kept approximately constant, the "territorial theory" of Eliot Howard (which is stated in a modified and more convincing form), the origin and meaning of bird song, courtship and breeding, migration, and the psychical nature of birds. All these topics are treated with sound biological insight on the basis of very wide personal observation and a thorough knowledge of the scattered literature. The theories and suggestions advanced nearly all commend themselves as the most reasonable interpretations of the facts given, and are in line with the most modern biological and psychological knowledge and thought. The style is vigorous, incisive and very fluent, if sometimes rather "breathless." The very low cost of the book ought to insure a large sale, and no ecologist or lover of nature will regret the minute expenditure of money and time involved in its purchase and in its perusal, from which he will certainly rise with a new knowledge of bird life. We wish Mr Nicholson many disciples, both in his acute and energetic observation and in his sound thinking.

I. A. R. I. 75.

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